Dentate *Gulella* of Madagascar (Pulmonata: Streptaxidae)

Kenneth C. Emberton

Florida Museum of Natural History, Box 117800, Gainesville, Florida 32611, U. S. A. ken_emberton@mailcity.com

Abstract: Based on collections made 1992-1996, 71 species and 8 subspecies of native Madagascan dentate *Gulella* Pfeiffer, 1856 (those having barriers or "teeth" in the aperture), can be recognized: *G. ambalaniranae* sp. nov.; *G. ambanikelia* sp. nov.; *G. ambatovakiae* sp. nov.; *G. ambrensis* sp. nov.; *G. ambrensis andavakoerae* subsp. nov.; *G. ambrensis capdambri* subsp. nov.; *G. ambrensis orangea* subsp. nov.; *G. ambrensis rakotomalalai* subsp. nov.; *G. analamerae* sp. nov.; *G. andreana* Fischer-Piette, Blanc and Vukadinovic, 1974; *G. ankaranensis* Fischer-Piette, Blanc, Blanc and Salvat, 1994; *G. antongilae* sp. nov.; *G. beandreana* sp. nov.; *G. bebokae* sp. nov.; *G. bemaraliae* sp. nov.; *G. bemoka* sp. nov.; *G. benjamini* Emberton and Pearce, 2000; *G. benjamini saintelucensis* subsp. nov.; *G. bobaombiae* sp. nov.; *G. bouchardi* Fischer-Piette, Blanc and Vukadinovic, 1974; *G. boucheti* Fischer-Piette, Blanc, Blanc and Salvat, 1994; *G. capmini* sp. nov.; *G. celestinae* sp. nov.; *G. columna* sp. nov.; *G. constricta* sp. nov.; *G. fischerpiettei* sp. nov.; *G. fischerpiettei enigma* subsp. nov.; *G. fotobolitrae* sp. nov.; *G. gallorum* Fischer-Piette, Blanc and Salvat, 1975; *G. griffithsi* sp. nov.; *G. hafa* sp. nov.; *G. hafahafa* sp. nov.; *G. jaominai* sp. nov.; *G. josephinae* sp. nov.; *G. kelibea* sp. nov.; *G. lohabea* sp. nov.; *G. lubeti* Fischer-Piette, Blanc, Blanc and Salvat, 1994; *G. magnifica* sp. nov.; *G. magnorchida* sp. nov.; *G. mahafinaratra* sp. nov.; *G. mahagaga* sp. nov.; *G. mahia* sp. nov.; *G. manomboae* sp. nov.; *G. marojejyae* sp. nov.; *G. masoalae* sp. nov.; *G. miaranoniae* sp. nov.; *G. miaryi* Fischer-Piette and Bedoucha, 1964; *G. michellae* sp. nov.; *G. microdon* (Morelet, 1860); *G. microstriata* sp. nov.; *G. mihomehia* sp. nov.; *G. mitsikia* sp. nov.; *G. nakamaroa* sp. nov.; *G. namorokae* sp. nov.; *G. nifikelia* sp. nov.; *G. nosybei* sp. nov.; *G. orchida* sp. nov.; *G. pearcei* sp. nov.; *G. petitboucheti* sp. nov.; *G. pseudandreana* sp. nov.; *G. rakotoarisoni* sp. nov.; *G. ranomasina* sp. nov.; *G. razafyi* sp. nov.; *G. reeae* Emberton and Pearce, 2000; *G. rubinsterni* Fischer-Piette, Blanc, Blanc and Salvat, 1994; *G. rugosa* sp. nov.; *G. satisfacta* Fischer-Piette, Blanc, Blanc and Salvat, 1994; *G. satisfacta charlesblanci* subsp. nov.; *G. satisfacta vitsia* subsp. nov.; *G. soulaiana* Fischer-Piette in Fischer-Piette, Cauquoin and Testud, 1973; *G. tendronia* sp. nov.; *G. tsara* sp. nov.; *G. tsaratananae* sp. nov.; *G. vakinifia* sp. nov.; *G. vatosoa* sp. nov.; *G. vavakelia* sp. nov.; *G. vohimarae* sp. nov.; and *G. zanaharyi* sp. nov. (*G. cerea* [Dunker, 1848], a Comoran species with a single unsubstantiated report from Madagascar, is dropped from the faunal list.)

A dichotomous key is given to these species plus the introduced *Gulella bicolor* (Hutton, 1834). Conchological descriptions are given of all the species. All species are illustrated except *G. bicolor, G. bouchardi, G. lubeti, G. miaryi, G. microdon, G. rubinsterni,* and *G. soulaiana*, for which refer to the *Faune de Madagascar* (Fischer-Piette *et al.*, 1994, vol. 83, pp. 1-551). Edentate *Gulella* of Madagascar (8 species) are treated in a separate paper.

Key Words: Gastropoda, Stylommatophora, land snails, taxonomy, shell variation

This paper is the second in a series on the conchological identification of Madagascar's lesser-known land-snail groups, based on extensive collections made in 1992-1996, and supplemental to the *Faune de Madagascar* monographs of Fischer-Piette *et al.* (1993, 1994). The first paper in the series treated the streptaxid genus *Edentulina* Pfeiffer, 1856 (11 species; Emberton, 1999). The third paper treats the alycaeid endemic genus *Boucardicus* Fischer-Piette and Bedoucha, 1965 (177 species, 6 subspecies; Emberton, in press a); the fourth treats the streptaxid endemic *Parvedentulina* Emberton and Pearce, 2000 (95 species) along with the conchologically similar edentate *Gulella* (8 species; Emberton, in press b); and other papers are in preparation.

Gulella Pfeiffer, 1856 (*sensu* Fischer-Piette *et al.*, 1994, who separate *Gonospira* Swainson, 1840), comprises one of the most diverse radiations within the widespread, carnivorous family Streptaxidae. Native *Gulella* seem to be restricted to Africa and Madagascar and adjacent islands, although some species have been introduced to other tropical regions (Zilch, 1959-1960; Richardson, 1988). The recent pulmonate gastropod volume of the *Faune de Madagascar* (Fischer-Piette *et al.*, 1994) summarized then current knowledge of that island's dentate *Gulella*, listing 13 species.

The author's survey of Madagascar's land molluscs (Emberton, 1994: fig. 1) was completed in 1996 and has resulted in extensive collections of dentate *Gulella* that are reported on here.

LOCALITIES

Of the 1,126 stations collected 1992-1996, the following 261 yielded *Gulella*. Station numbers are in the MBI series. Person-hours refer to actual search time for specimens at the station. Liters of litter refer to the

unsieved volume of litter or litter-plus-soil that was collected and later dried, sieved, and sorted.

6. Forêt Ste. Luce, 24°46'30"S, 47°09'00"E, 10 m, coastal rainforest, 29-Jan-95, 6 person-hr.

31. Manombo Reserve, 23°00'50"S, 47°44'00"E, 50 m, rainforest, 20-Apr-95, 27 person-hr.

32. Miaranony, E Ranomafana National Park, 21°10'05"S, 47°33'20"E, 630 m, rainforest, 25-Apr-95, 10 person-hr.

42. E. Morondava, 20°23'35"S, 44°48'05"E, 75 m, dry deciduous forest, 11-May-95, 2 person-hr, 4 l litter.

43. 6.8 W Ankilozato, 20°22'15"S, 45°00'11"E, 205 m, riverine deciduous forest, 11-May-95, 4 person-hr, 3 l litter.

49. 9.6 SSW Mania River bridge, 19°49'59"S, 45°31'12"E, 65 m, gully forest of palmetto and scrub, 12-May-95, 3 person-hr, 2 l litter.

52. 0.2km E Antanandava, 16°07'40"S, 45°28'40"E, 40 m, scrub forest, 18-May-95.

55-74. Namoroka Reserve. 55. 16°23'00"S, 45°21'30"E, 110 m, dry deciduous forest, 21-May-95, 185 person-hr, 4 l litter. 56. 16°21'48"S, 45°19'04"E, 100 m, dry deciduous-baobab forest, 22-May-95, 176 person-hr, 2 l litter. 58. 16°25'18"S, 45°23'27"E, 120 m, dry deciduous forest, 23-May-95, 28 person-hr. 61. 16°23'20"S, 45°18'25"E, 105 m, dry deciduous forest, 25-May-95, 176 person-hr, 1 l litter. 62. 16°24'00"S, 45°17'58"E, 90 m, hardwood forest, 26-May-95, 144 person-hr. 63. 16°23'07"S, 45°18'41"E, 75 m, dry deciduous forest, 27-May-95, 3 l litter. 64. 16°23'26"S, 45°18'10"E, 90 m, raffia swamp, 27-May-95, 42 person-hr, 2 l litter. 65. 16°23'26"S, 45°18'10"E, 90 m, raffia swamp, 27-May-95, 45 person-hr. 67. 16°23'15"S, 45°20'45"E, 110 m, dry deciduous forest, 24-May-95, 47 person-hr, 1 l litter. 68. 16°22'50"S, 45°20'50"E, 85 m, dry deciduous forest, 24-May-95, 45 person-hr, 1 l litter. 69. 16°22'35"S, 45°19'30"E, 95 m, dry deciduous forest, 25-May-95, 76 person-hr, 1 l litter. 70. 16°22'35"S, 45°20'05"E, 115 m, dry deciduous forest, 25-May-95, 60 person-hr, 1 l litter. 71. 16°23'45"S, 45°21'30"E, 100 m, dry deciduous forest, 26-May-95, 72 person-hr, 1 l litter. 72. 16°23'30"S, 45°21'15"E, 125 m, dry deciduous forest, 26-May-95, 34 person-hr, 1 l litter. 73. 16°24'50"S, 45°20'55"E, 115 m, dry deciduous forest, 27-May-95, 10 person-hr, 1 l litter. 74. 16°23'00"S, 45°20'20"E, 100 m, dry deciduous forest, 28-May-95, 14 person-hr, 2 l litter.

81-84. Ampijoroa Reserve, 16°17'28"S, 46°49'13"E, 20 m, dry deciduous forest, 2-Jun-95, 4 person-hr, 2 l litter. 82. 16°17'18"S, 46°49'16"E, 20 m, dry deciduous forest, 2-Jun-95, 14 person-hr, 2 l litter. 83. 16°17'19"S, 46°49'35"E, 95 m, hardwood deciduous forest, 3-Jun-95, 102 person-hr, 3 l litter. 84. 16°17'01"S, 46°49'12"E, 85 m, dry deciduous forest, 4-Jun-95, 2 person-hr, 2 l litter.

95-115. Tsaratanana Reserve. 95. 14°02'35"S, 48°46'28"E, 1160 m, rainforest, 13-Jun-95, 7 person-hr, 1 l litter. 98. 14°02'52"S, 48°47'09"E, 950 m, rainforest, 14-Jun-95, 28 person-hr. 103. 14°02'12"S, 48°46'20"E, 865 m, rainforest, 16-Jun-95, 10 person-hr. 105. 14°02'12"S, 48°46'15"E, 770 m, rainforest, 16-Jun-95, 7 person-hr. 106. 14°02'12"S, 48°46'15"E, 740 m, rainforest, 17-Jun-95, 10 person-hr. 107. 14°02'00"S, 48°46'07"E, 685 m, rainforest, 17-Jun-95. 108. 14°01'50"S, 48°46'00"E, 630 m, rainforest, 17-Jun-95, 16 person-hr. 110. 14°01'40"S, 48°45'50"E, 540 m, rainforest, 18-Jun-95, 10 person-hr. 111. 14°01'40"S, 48°45'45"E, 500 m, rainforest, 18-Jun-95, 10 person-hr. 112. 14°01'40"S, 48°45'40"E, 480 m, rainforest, 18-Jun-95, 12 person-hr. 114. 14°01'40"S, 48°45'35"E, 445 m, rainforest, 19-Jun-95, 5 person-hr. 115. 14°01'35"S, 48°45'35"E, 420 m, rainforest, 19-Jun-95, 1 person-hr.

118. Lokobe Reserve, 13°25'00"S, 48°18'40"E, 60 m, rainforest, 25-Jun-95, 15 person-hr, 3 l litter.

168. Galoko Escarpment, 13°34'30"S, 48°45'16"E, 225 m, hardwood-palm-pandanus forest, 4-Jul-95, 14 person-hr, 2 l litter.

170-195. Montagne d'Ambre National Park. 170. 12°32'55"S, 49°09'50"E, 1250 m, 8-Jul-95, 5 person-hr. 172. 12°35'46"S, 49°09'35"E, 1325 m, montane rainforest, 8-Jul-95, 15 person-hr, 2 l litter. 178. 12°37'09"S, 49°10'26"E, 1135 m, montane rainforest, 9-Jul-95, 6 person-hr, 2 l litter. 181. 12°37'22"S, 49°10'28"E, 1040 m, rainforest, 9-Jul-95, 17 person-hr, 2 l litter. 182. 12°37'25"S, 49°10'30"E, 1095 m, montane rainforest, 10-Jul-95, 5 person-hr, 2 l litter. 184. 12°36'46"S, 49°09'57"E, 1165 m, rainforest, 10-Jul-95, 14 person-hr, 2 l litter. 185. 12°36'35"S, 49°09'52"E, 1205 m, rainforest, 10-Jul-95, 6 person-hr, 2 l litter. 192. 12°35'04"S, 49°08'46"E, 1235 m, rainforest, 12-Jul-95, 6 person-hr, 2 l litter. 193. 12°34'34"S, 49°09'25"E, 1305 m, rainforest, 12-Jul-95, 6 person-hr, 2 l litter. 195. 12°31'42"S, 49°10'16"E, 1050 m, rainforest, 12-Jul-95, 9 person-hr, 2 l litter.

199-214. Analamera Reserve. 199. 12°43'46"S, 49°28'50"E, 35 m, dry deciduous forest, 15-Jul-95, 7 person-hr, 2 l litter. 201. 12°44'28"S, 49°30'21"E, 315 m, dry deciduous forest, 15-Jul-95, 30 person-hr, 2 l litter. 202. 12°44'32"S, 49°30'20"E, 310 m, dry deciduous forest, 16-Jul-95. 203. 12°44'35"S, 49°30'16"E, 285 m, bamboo-dry deciduous thicket, 16-Jul-95, 11 person-hr, 2 l litter. 204. 12°44'38"S, 49°30'13"E, 235 m, dry deciduous forest, 16-Jul-95, 11 person-hr, 2 l litter. 206. 12°44'42"S, 49°30'08"E, 195 m, dry deciduous forest, 16-Jul-95, 11 person-hr, 2 l litter. 207. 12°44'43"S, 49°30'06"E, 150 m, dry deciduous forest, 16-Jul-95. 208. 12°44'45"S, 49°30'04"E, 100 m, dry deciduous forest, 16-Jul-95, 6 person-hr, 2 l litter. 210. 12°44'49"S, 49°29'57"E, 35 m, dry deciduous floodplain forest, 16-Jul-95, 8 person-hr, 2 l litter. 212. 12°43'46"S, 49°28'53"E, 35 m, 16-Jul-95. 213. 12°44'50"S, 49°29'40"E, 30 m, dry deciduous floodplain forest, 16-Jul-95, 30 person-hr, 2 l litter. 214. 12°42'09"S, 49°27'61"E, 20 m, dry deciduous forest, 16-Jul-95, 5 person-hr, 2 l litter.

215-218. Montagne des Orchides. 215. 12°23'31"S, 49°19'41"E, 295 m, dry deciduous forest, 20-Jul-95, 14 person-hr, 2 l litter. 217. 12°23'23"S, 49°19'45"E, 360 m, dry deciduous forest, 20-Jul-95, 18 person-hr, 2 l litter. 218. 12°23'25"S, 49°19'48"E, 385 m, dry deciduous forest, 20-Jul-95, 16 person-hr, 2 l litter.

221. Montagne des Français. 221. 12°19'30"S, 49°20'22"E, 300 m, secondary dry deciduous forest, 21-Jul-95, 12 person-hr, 3 l litter. 222. 12°19'20"S, 49°20'20"E, 230 m, dry deciduous forest, 21-Jul-95, 5 person-hr, 2 l litter. 223. 12°18'55"S, 49°20'15"E, 70 m, dry deciduous forest, 21-Jul-95, 3 person-hr, 1 l litter.

224-225. Baie des Dunes, Cap Mine, edge of Forêt d'Orange. 224. 12°14'40"S, 49°22'43"E, 03 m, scrub, 21-Jul-95, 4 person-hr, 2 l litter. 225. Baie des Dunes, 12°14'20"S, 49°22'25"E, 06 m, scrub, 21-Jul-95, 1 person-hr, 2 l litter.

229-241. N Cap d'Ambre. 229. near lighthouse, 11°57'30"S, 49°16'35"E, 05 m, euphorb scrub forest, 24-Jul-95, 9 person-hr, 2 l litter. 230. near lighthouse, 11°57'48"S, 49°16'33"E, 20 m, dry deciduous forest, 24-Jul-95, 5 person-hr, 2 l litter. 233. near lighthouse, 11°58'00"S, 49°16'40"E, 10 m, deciduous-baobab forest, 24-Jul-95, 11 person-hr, 2 l litter. 234. near Bemoka, 11°59'00"S, 49°16'30"E, 25 m, dry deciduous forest, 24-Jul-95, 6 person-hr, 2 l litter. 238. near Ambatojanahary, 12°00'14"S, 49°17'52"E, 40 m, baobab-deciduous forest, 25-Jul-95, 49 person-hr, 2 l litter. 239. near Ambatojanahary, 12°00'10"S, 49°17'50"E, 40 m, dry deciduous forest, 25-Jul-95, 22 person-hr, 2 l litter. 240. near Ambatojanahary, 12°00'00"S, 49°17'50"E, 05 m, dry deciduous forest, 25-Jul-95, 12 person-hr, 2 l litter. 241. near Ambatojanahary, 12°00'03"S, 49°17'27"E, 15 m, dry deciduous forest, 25-Jul-95, 6 person-hr, 2 l litter.

245-255. S Bemaraha Reserve. 245. 19°08'36"S, 44°48'54"E, 70 m, dry forest, 14-Jun-95, 9 person-hr, 6 l litter. 247. 19°08'06"S, 44°52'54"E, 100 m, lush tall riverine gallery forest, 15-Jun-95, 9 person-hr. 248. 19°07'36"S, 44°52'54"E, 100 m, lush tall riverine gallery forest, 15-Jun-95, 4 person-hr. 249. 19°08'06"S, 44°50'36"E, 100 m, tall riverine gallery forest, 16-Jun-95, 4 person-hr. 250. 19°08'12"S, 44°49'42"E, 80 m, tall riverine gallery forest, 16-Jun-95, 3 person-hr. 251. 19°07'36"S, 44°48'36"E, 70 m, dry forest, 17-Jun-95, 8 person-hr. 252. 19°07'48"S, 44°48'54"E, 70 m, dry, flood prone forest, 17-Jun-95, 2 person-hr. 254. 19°02'24"S, 44°48'00"E, 150 m, forest along limestone wall, 18-Jun-95, 6

person-hr. 255. 19°00'48"S, 44°46'54"E, 150 m, tall forest in limestone slots, 19-Jun-95, 9 person-hr.

256-257. S of Vohimar, 13°35'05"S, 49°59'32"E, viny rainforest, 2-Sep-95. 256. 90 m, 8 person-hr, 2 l litter. 257. 70 m, 1 person-hr.

258-267. Ambalanirana Mountain. 258. 13°50'56"S, 49°59'27"E, 210 m, rainforest, 3-Sep-95, 27 person-hr, 2 l litter. 259. 13°50'S, 49°59'E, 350 m, rainforest, 3-Sep-95. 260. 13°50'S, 49°59'E, 561 m, rainforest, 3-Sep-95, 31 person-hr, 2 l litter. 261. 13°50'S, 49°59'E, 500 m, rainforest, 4-Sep-95, 47 person-hr, 2 l litter. 262. 13°50'S, 49°59'E, 400 m, viny rainforest, 4-Sep-95, 56 person-hr, 2 l litter. 263. 13°50'S, 49°59'E, 400 m, rainforest, 4-Sep-95. 264. 13°50'S, 49°59'E, 300 m, palm rainforest, 4-Sep-95, 68 person-hr, 2 l litter. 265. 13°50'44"S, 49°59'48"E, 465 m, palm rainforest, 5-Sep-95, 38 person-hr, 2 l litter. 266. 13°50'S, 49°59'E, 400 m, rainforest, 5-Sep-95, 38 person-hr, 2 l litter. 267. 13°50'S, 49°59'E, 315 m, rainforest, 5-Sep-95, 68 person-hr, 2 l litter.

270. Andranomena Forest, N of Sambava, 13°56'29"S, 50°05'02"E, 20 m, rainforest, 8-Sep-95, 22 person-hr, 2 l litter.

279-314. W Masoala Peninsula. 279. 15°54'50"S, 50°04'20"E, 60 m, hardwood-pandanus rainforest, 15-Sep-95, 18 person-hr. 282. 15°52'55"S, 50°01'11"E, 50 m, hardwood rainforest, 15-Sep-95, 10 person-hr. 283. 15°52'45"S, 50°01'55"E, 60 m, hardwood rainforest, 16-Sep-95, 17 person-hr, 2 l litter. 284. 15°52'20"S, 50°02'15"E, 05 m, hardwood-pandanus rainforest, 16-Sep-95, 9 person-hr. 285. 15°52'15"S, 50°02'15"E, 20 m, hardwood rainforest, 16-Sep-95, 9 person-hr. 289. 15°51'00"S, 50°02'00"E, 180 m, hardwood-pandanus-palm rainforest, 16-Sep-95, 9 person-hr. 294. 15°48'25"S, 50°03'05"E, 130 m, hardwood-palm forest, 18-Sep-95, 38 person-hr, 2 l litter. 295. 15°48'05"S, 50°03'10"E, 310 m, hardwood-pandanus forest, 18-Sep-95, 42 person-hr, 2 l litter. 300. 15°47'20"S, 50°03'50"E, 350 m, hardwood rainforest, 20-Sep-95, 39 person-hr, 2 l litter. 303. 15°48'22"S, 50°03'00"E, 220 m, hardwood-palm rainforest, 22-Sep-95, 44 person-hr, 2 l litter. 306. 15°33'S, 50°00'E, 430 m, 25-Sep-95. 307. 15°33'45"S, 50°00'15"E, 680 m, hardwood rainforest, 25-Sep-95, 66 person-hr, 2 l litter. 310. 15°33'45"S, 50°00'25"E, 840 m, hardwood-pandanus forest, 26-Sep-95, 45 person-hr, 2 l litter. 311. 15°33'30"S, 49°59'50"E, 430 m, hardwood rainforest, 27-Sep-95, 45 person-hr. 313. 15°33'27"S, 49°59'40"E, 305 m, hardwood rainforest, 28-Sep-95, 45 person-hr, 2 l litter. 314. 15°33'25"S, 49°59'25"E, 180 m, hardwood rainforest, 28-Sep-95, 45 person-hr, 2 l litter.

342. Mt. Mahalevona, E of Maroantsetra, 15°25'12"S, 49°57'05"E, 925 m, hardwood-palm rainforest, 11-Oct-95, 28 person-hr, 2 l litter.

349-358. W of Sahasoa, S of Mananara. 349. 16°19'20"S, 49°44'55"E, 480 m, hardwood rainforest, 18-Oct-95, 57 person-hr, 4 l litter. 351. 16°19'35"S, 49°44'30"E, 515 m, hardwood-pandanus forest, 18-Oct-95, 36 person-hr, 2 l litter. 353. 16°19'35"S, 49°44'00"E, 465 m, hardwood rainforest, 19-Oct-95, 47 person-hr, 2 l litter. 354. 16°19'35"S, 49°44'25"E, 515 m, hardwood-pandanus forest, 19-Oct-95, 14 person-hr. 355. 16°19'35"S, 49°44'29"E, 510 m, hardwood-pandanus forest, 19-Oct-95, 17 person-hr. 356. 16°19'37"S, 49°45'57"E, 350 m, hardwood-pandanus forest, 20-Oct-95, 36 person-hr. 357. 16°19'20"S, 49°46'50"E, 330 m, hardwood rainforest, 21-Oct-95, 30 person-hr. 358. 16°19'30"S, 49°47'45"E, 330 m, hardwood-ravenala forest, 21-Oct-95, 27 person-hr, 2 l litter.

363-364. NW of Manompona, S of Mananara 363. 16°39'50"S, 49°40'40"E, 240 m, hardwood rainforest, 24-Oct-95, 30 person-hr, 1 l litter. 364. 16°39'48"S, 49°41'25"E, 160 m, hardwood rainforest, 25-Oct-95, 3 person-hr.

366-367. Isle Ste. Marie. 366. 16°55'07"S, 49°53'15"E, 110 m, hardwood-palm-ravenala forest, 26-Oct-95, 14 person-hr, 2 l litter. 367. 16°54'45"S, 49°53'05"E, 80 m, hardwood-palm-ravenala forest, 27-Oct-95, 14 person-hr.

400-401. S Cap d'Ambre, la Butte Bobaomby. 400. 12°10'55"S, 49°13'00"E, 70 m, dry deciduous forest, 24-Aug-95, 8 person-hr, 2 l litter. 401. 12°11'45"S, 49°13'00"E, 205 m, dry deciduous-baobab forest, 24-Aug-95, 32 person-hr, 2 l litter.

403-407. S Cap d'Ambre, Ambongoabo. 403. 12°15'55"S, 49°15'20"E, 352 m, scrub, 25-Aug-95, 4 person-hr, 1 l litter. 404. 12°15'55"S, 49°15'20"E, 340 m, dry deciduous forest, 25-Aug-95, 6 person-hr, 2 l litter. 405. 12°15'55"S, 49°15'27"E, 320 m, baobab-deciduous forest, 25-Aug-95, 12 person-hr. 407. 12°15'55"S, 49°15'40"E, 290 m, dry deciduous forest, 26-Aug-95, 5 person-hr, 2 l litter.

408-411. W of Sakaramy, S of Diego Suarez. 408. 12°26'35"S, 49°13'15"E, 410 m, dry deciduous forest, 26-Aug-95, 20 person-hr, 2 l litter. 411. 12v26'35"S, 49°12'45"E, 380 m, dry deciduous forest, 26-Aug-95, 12 person-hr, 2 l litter.

413-421. Andavakoera, N of Betsiaka. 413. 13°07'44"S, 49°14'05"E, 240 m, dry deciduous forest, 30-Aug-95, 26 person-hr, 2 l litter. 417. 13°06'36"S, 49°13'23"E, 230 m, dry deciduous forest, 30-Aug-95, 62 person-hr, 2 l litter. 418. 13°06'24"S, 49°13'19"E, 115 m, dry deciduous forest, 31-Aug-95, 115 person-hr, 2 l litter. 421. 13°07'S, 49°13'E, 410 m, dry deciduous forest, 1-Sep-95, 26 person-hr, 2 l litter.

423-435. Manombo Reserve, 23°00'50"S, 47°44'00"E, 50 m, rainforest. 423. 21-Apr-95, 528 person-hr. 424. 22-May-95, 256 person-hr. 425. 30-Jun-95, 256 person-hr. 426. 23-Jul-95, 256 person-hr. 427. 23-Aug-95, 256 person-hr. 428. 22-Sep-95, 256 person-hr. 429. 22-Oct-95, 256 person-hr. 430. 22-Nov-95, 256 person-hr, 40 l litter. 431. 22-Dec-95, 256 person-hr. 432. 23-Jan-96, 256 person-hr. 433. 27-Feb-96, 256 person-hr. 434. 23-Mar-96, 256 person-hr. 435. 22-Apr-96, 256 person-hr, 40 l litter.

439-451. Miaranony, E Ranomafana National Park, 21°10'05"S, 47°33'20"E, 630 m, rainforest. 439. 26-Apr-95, 520 person-hr. 440. 27-May-95, 256 person-hr. 441. 5-Jul-95, 256 person-hr. 442. 29-Jul-95, 256 person-hr. 443. 29-Aug-95, 248 person-hr. 444. 28-Sep-95, 248 person-hr. 445. 29-Oct-95, 248 person-hr. 446. 28-Nov-95, 248 person-hr, 40 l litter. 447. 29-Dec-95, 256 person-hr. 448. 28-Jan-96, 248 person-hr. 449. 2-Mar-96, 240 person-hr. 450. 29-Mar-96, 256 person-hr. 451. 28-Apr-96, 256 person-hr, 40 l litter.

458-466. Ambatolahy, next to Ranomafana National Park, 21°13'50"S, 47°25'20"E, 850 m, rainforest. 458. 9-Sep-95, 248 person-hr. 459. 9-Oct-95, 248 person-hr. 460. 9-Nov-95, 248 person-hr, 40 l litter. 461. 14-Dec-95, 248 person-hr. 462. 9-Jan-96, 248 person-hr. 463. 9-Feb-96, 248 person-hr. 464. 9-Mar-96, 248 person-hr. 465. 10-Apr-96, 248 person-hr. 466. 9-May-96, 248 person-hr, 40 l litter.

483-494. N Bemaraha Reserve. 483. 18°01'48"S, 44°31'42"E, 270 m, dry deciduous forest, 22-Jun-96. 484. 18°03'30"S, 44°31'42"E, 250 m, dry deciduous forest, 23-Jun-96. 489. 18°41'36"S, 44°43'06"E, 150 m, semideciduous forest, 27-Jun-96. 490. 18°45'24"S, 44°45'24"E, 280 m, semideciduous forest, 27-Jun-96. 494. 18°45'54"S, 44°45'24"E, 280 m, semideciduous forest, 29-Jun-96.

502-540. Tsaratanana Reserve. 502. 14°01'30"S, 48°45'08"E, 310 m, rainforest, 12-Jun-95, 4 person-hr, 1 l litter. 503. 14°00'58"S, 48°46'10"E, 600 m, rainforest, 12-Jun-95, 5 person-hr, 1 l litter. 504. 14°00'42"S, 48°46'30"E, 730 m, rainforest, 13-Jun-95, 10.5 person-hr, 0.5 l litter. 505. 14°00'24"S, 48°46'30"E, 910 m, rainforest, 13-Jun-95, 10.5 person-hr, 0.5 l litter. 513. 13°59'45"S, 48°47'25"E, 1525 m, rainforest, 14-Jun-95, 7 person-hr, 1 l litter. 514. 13°59'40"S, 48°47'10"E, 1660 m, cloudforest, 14-Jun-95, 4 person-hr, 1 l litter. 527. 13°59'05"S, 48°47'40"E, 1395 m, rainforest, 17-Jun-95, 13 person-hr, 1 l litter. 535. 13°59'20"S, 48°46'32"E, 930 m, rainforest, 18-Jun-95, 6 person-hr, 0.5 l litter. 537. 14°00'06"S, 48°46'30"E, 810 m, savannah, 19-Jun-95, 2 person-hr, 1 l litter. 538. 14°00'04"S, 48°46'35"E, 790 m, rainforest, 19-Jun-95, 7 person-hr, 1 l litter. 540. 14°00'58"S, 48°46'25"E, 700 m, rainforest, 19-Jun-95, 2 person-hr, 1 l litter.

546. Nosy Komba, 13°26'25"S, 48°20'30"E, 10 m, scrub, 23-Jun-95, 2 person-hr.

554-581. Ankarana Reserve. 554. 12°55'35"S, 49°06'55"E, 70 m, dry deciduous forest, 21-Aug-95, 15 person-hr, 2 l litter. 558. 12°54'33"S, 49°06'37"E, 80 m, dry deciduous forest, 22-Aug-95, 14 person-hr, 2 l litter. 561. 12°55'35"S, 49°05'39"E, 30 m, dry deciduous forest, 22-Aug-95, 12 person-hr, 2 l litter. 564. 12°55'26"S, 49°05'12"E, 95 m, dry deciduous forest, 22-Aug-95, 19 person-hr, 2 l litter. 565. 12°55'33"S, 49°05'28"E, 40 m, dry deciduous forest, 22-Aug-95, 10 person-hr, 2 l litter. 566. 12°56'09"S, 49°07'13"E, 90 m, dry deciduous forest, 23-Aug-95, 14 person-hr, 2 l litter. 568. 12°56'43"S, 49°07'29"E, 125 m, dry deciduous forest, 23-Aug-95, 6 person-hr, 4 l litter. 570. 12°57'22"S, 49°07'05"E, 45 m, dry deciduous forest, 24-Aug-95, 6 person-hr, 2 l litter. 571. 12°57'24"S, 49°07'05"E, 85 m, dry deciduous forest, 24-Aug-95, 9 person-hr, 2 l litter. 572. 12°57'26"S, 49°07'05"E, 110 m, dry deciduous forest, 24-Aug-95, 5 person-hr, 2 l litter. 576. 12°58'26"S, 49°06'54"E, 90 m, dry deciduous forest, 25-Aug-95, 10 person-hr, 2 l litter. 577. 12°58'39"S, 49°06'30"E, 100 m, dry deciduous forest, 25-Aug-95, 13 person-hr, 2 l litter. 579. 12°58'53"S, 49°06'03"E, 100 m, dry deciduous forest, 25-Aug-95, 14 person-hr, 2 l litter. 580. 12°58'56"S, 49°05'49"E, 95 m, dry deciduous forest, 26-Aug-95, 21 person-hr, 4 l litter. 581. 12°58'50"S, 49°06'35"E, 110 m, dry deciduous forest, 26-Aug-95, 6.5 person-hr, 2 l litter.

593-612. Marojejy Reserve. 553. 14°26'12"S, 49°44'36"E, 1300 m, rainforest, 14-Sep-95, 12 person-hr, 2 l litter. 612. 14°26'05"S, 49°46'20"E, 520 m, rainforest, 18-Sep-95, 16 person-hr, 2 l litter.

627-649. W Marojejy Reserve. 627. 14°28'00"S, 49°35'30"E, 900 m, rainforest, 25-Sep-95, 7 person-hr, 2 l litter. 634. 14°28'10"S, 49°35'30"E, 1170 m, rainforest, 25-Sep-95, 14 person-hr, 2 l litter. 645. 14°28'53"S, 49°33'40"E, 960 m, rainforest, 27-Sep-95, 6 person-hr, 2 l litter. 648. 14°29'20"S, 49°33'35"E, 805 m, rainforest, 28-Sep-95, 23 person-hr, 2 l litter. 649. 14°29'40"S, 49°34'00"E, 700 m, rainforest, 28-Sep-95, 24 person-hr, 2 l litter.

650-677. E of Marojejy Reserve. 650. 14°S, 49°E, 200 m, moist forest, 29-Sep-95. 661. 14°32'38"S, 49°42'15"E, 1100 m, rainforest, 4-Oct-95, 6 person-hr, 2 l litter. 666. 14°32'38"S, 49°42'05"E, 1400 m, cloudforest with bamboo, 5-Oct-95, 8 person-hr, 4 l litter. 668. 14°32'39"S, 49°42'00"E, 1500 m, cloudforest with bamboo, 5-Oct-95, 5 person-hr, 4 l litter. 671. 14°32'37"S, 49°42'14"E, 1300 m, rainforest, 5-Oct-95, 7 person-hr, 4 l litter. 674. 14°32'30"S, 49°42'10"E, 880 m, rainforest, 6-Oct-95, 10 person-hr, 4 l litter. 677. 14°31'35"S, 49°43'55"E, 315 m, rainforest, 7-Oct-95, 10 person-hr, 4 l litter.

679. 2km N Mandena, ca 14°28'S, ca 49°55'E, 15-Oct-95, 40 person-hr.

680. 5km NE Manantenina, 14°27'S, 49°49'E, 16-Oct-95, 40 person-hr.

711-714. near Ampanifena, near Mt. Ambalanirana, 13°51'S, 49°59'E, 25-Oct-95. 711. 300 m, 192 person-hr. 712. 350 m, 840 person-hr. 714. 300 m, 32 person-hr.

715-717. near Mandena, ca 14°28'S ca 49°55'E, 25-Oct-95. 715. 25-Oct-95, 16 person-hr, 5 l litter. 716. 16 person-hr, 2 l litter. 717. 16 person-hr, 4 l litter.

723-724. Soanierana Ivongo. 723. 16°55'30"S, 49°35'12"E, 20 m, introduced eucalyptus forest, 11-Nov-95, 3 person-hr, 3 l litter. 724. 16°55'32"S, 49°35'12"E, 60 m, degraded scrub, 11-Nov-95, 2 person-hr, 2 l litter.

742-766. Ambatovaky Reserve. 742. 16°47'17"S, 49°08'11"E, 890 m, rainforest with pandanus, 20-Nov-95, 16 person-hr, 4 l litter. 744. 16°46'58"S, 49°08'21"E, 1025 m, rainforest with pandanus, 21-Nov-95, 10 person-hr, 8 l litter. 756. 16°44'47"S, 49°10'38"E, 675 m, rainforest with pandanus, 22-Nov-95, 5 person-hr, 2 l litter. 758. 16°42'50"S, 49°10'27"E, 605 m, rainforest, 23-Nov-95, 7 person-hr, 2 l litter. 766. 16°43'26"S, 49°23'10"E, 400 m, rainforest, 27-Nov-95, 6 person-hr, 2 l litter.

802-816. Ankarana Reserve. 802. 13°00'18"S, 49°00'18"E, 50 m, 8-Oct-94. 803. 13°00'00"S, 49°01'00"E, 50 m, 8-Oct-94. 805. 13°01'24"S, 49°00'00"E, 50 m, 8-Oct-94. 807. 12°54'24"S, 49°06'42"E, 90 m, 10-Oct-94. 810. 12°54'54"S, 49°06'18"E, 90 m, 10-Oct-94. 813. 12°57'54"S, 49°08'18"E, 150 m, 11-Oct-94. 814. 12°56'48"S, 49°07'42"E, 70 m, 11-Oct-94. 815. 12°55'42"S, 49°03'18"E, 100 m, 12-Oct-94. 816. 12°55'48"S, 49o03'18"E, 100 m, 12-Oct-94.

818. Betsiboka River, 16°57'S, 46°57'E, 135 m, 14-Oct-94.

1342. 23.9 km S of Farafangana, 23°00'00"S, 47°44'30"E, 60 m, 14-Sep-92, 28 person-hr.

1347-1351. Manombo Reserve. 1347. 23°01'40"S, 47°44'00"E, 50 m, 15-Sep-92. 1351. 23°01'00"S, 47°44'00"E, 50 m, native forest, 16-Sep-92, 480 person-hr.

1389-1391. Fotobohitra, 21°21'40"S, 47°51'20"E, 27-Sep-92. 1389. 350 m, rainforest, 16 person-hr. 1391. 320 m, ravenala forest, 6 person-hr.

1402. near Andringitra Reserve, 22°04'S, 46°54'E, 1400 m, primary forest, 3-Oct-92, 36 person-hr.

1419. Pic Saint Louis, near Ft. Dauphin, 25°00'30"S, 46°57'45"E, rainforest, 530 m, 10-Oct-92, 5 person-hr.

1529-1549. Betampona Reserve, rainforest. 1529. 17°54'15"S, 49°12'40"E, 600 m, 13-May-93, 1.7 person-hr. 1536. 17°54'00"S, 49°12'35"E, 540 m, 14-May-93, 9 person-hr. 1540. 17°54'25"S, 49°13'25"E, 530 m, 15-May-93, 4 person-hr. 1545. 17°55'15"S, 49°13'15"E, 560 m, 16-May-93, 4 person-hr. 1547. 17°55'35"S, 49°13'10"E, 400 m, 16-May-93, 6 person-hr. 1549. 17°54'S, 49°12'E, 400 m, 16-May-93.

METHODS AND MATERIALS

Materials were collected 1992-1996, using methods advocated in Emberton *et al.* (1996).

Table 1 and Fig. 1 show the characters used. Because of Madagascar's continuing environmental crisis and the urgency it puts upon providing taxonomic data to conservationists and systematists, I have examined only shell morphology and have generally assessed characters visible only in apertural and apical views. Despite these restrictions, the resulting 30 characters (Fig. 1, Table 1) seemed adequate, with key additions in a few special cases (Tables 2 and 4), for an initial pass at delimiting taxa within this complex and rather difficult group.

I have attempted to apply Templeton's (1989) cohesion concept of species. Disjunct shell morphologies occurring in sympatry with no intermediates I considered distinct species (there is no sexual dimorphism, as *Gulella* are hermaphroditic). I then used the degrees of conchological differences between such sympatric species as guidelines for delimiting allopatric species, also comparing ecologies and searching for additional shell characters to resolve borderline cases.

Within especially variable species, I selected not only a standard representative but also one to three extreme variants for description and/or illustration. Geographically separated, morphologically discrete, extreme variants I deemed subspecies only if they seemed well isolated by discontinuous habitat. I photographed shells at standard

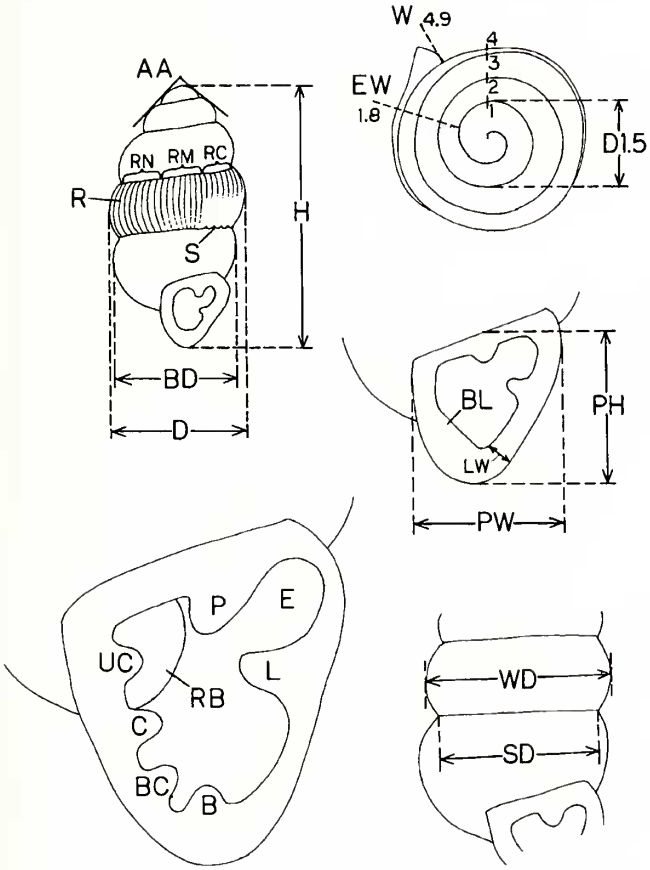


Fig. 1. Characters (see Table 1). Abbreviations: AA, apical angle; B, baso-central tooth; BC, baso-columellar tooth; BD, body-whorl diameter; BL, baso-columellar lamella; C, mid-columellar tooth; D, mid-shell greatest diameter; D1.5, diameter of first 1.5 whorls; E, parieto-palatal embayment; EW, embryonic whorl count; H, shell height; L, palatal tooth; LW, apertural lip width; P, parietal tooth; PH, peristome height; PW, peristome width, R, rib sculpture, RB, columellar recessed baffle; RC, complete diminution of rib sculpture; RM, moderate diminution of rib sculpture; RN, no diminution of rib sculpture; S, sutural crenulation; SD, sutural diameter; UC, upper-columellar tooth; W, whorl count; WD, whorl diameter used in calculating sutural depth.

magnifications (6.4x, 10x, 16x, 25x, and 40x) in apertural view. For identifications and diagnoses, I referred to Fischer-Piette *et al.* (1994) and Emberton and Pearce (2000) for Madagascar; Griffiths (1996, and his unpublished, illustrated catalog) for the Mascarenes; Hanley and Theobald (1876) and Blanford and Godwin-Austen (1908) for India and Sri Lanka; and Moellendorff and Kobelt (1905), Pilsbry (1919), Germain (1923), Connolly (1939), Verdcourt (1961-1993), Bruggen (1965-1980), and Winter (1996) for Africa, Aldabra, and the Comoros.

RESULTS

Table 2 compares the 14 most similar sympatric-species pairs I detected. The 7 pairs diagnosable by apertur-

Table 1. Characters used (see Fig. 1). Measurements were taken by ocular micrometer on a dissecting microscope or by millimeter rule on a photograph. For maximum accuracy, all ratios were calculated using unconverted measurement units. Some additional shell characters used in distinguishing cryptic species and subspecies are given in Tables 2 and 4.

Shell Size and Shape

1) Height (H), to 0.1 mm
2) Diameter (D), mid-shell greatest, to 0.1 mm
3) Height/diameter = H/D, to 0.1
4) Whorl count (W), starting at the engraved, straightish line marking the beginning of the suture, as seen at 40x magnification under narrow-beam, perpendicular side lighting, to 0.1 whorl (0.05 whorl for Table 3)
5) Coiling-tightness index = W/lnH, where W = whorl count, H = shell height, and ln = natural logarithm (base e)
6) Apical angle (AA), to 5°
7) Barreling index (percent barreling) = 100((D-BD)/D), where D = greatest mid-shell diameter, and BD = the body-whorl diameter above and not including the peristome

Suture and Sculpture of Penultimate and Body Whorls

8) Sutural depth index = 100((WD-SD)/WD), where SD = diameter along a major suture, and WD = parallel greatest diameter of the whorl just above that suture
9) Sutural crenulation (S): none, weak, moderate, or strong
10) Rib-sculpture (R) strength near upper suture: none, weak, moderate, or strong
11) Rib-sculpture diminishment from upper suture to lower suture: none (RN), moderate (RM), or complete (RC)

Embryonic Shell Size and Sculpture

12) Embryonic whorl count (EW), to 0.1 whorl
13) Diameter of first 1.5 whorls (D1.5), measured at 40x magnification, to 0.01 mm (0.001 mm for Table 3)
14) Embryonic sculpture as seen at 40x magnification under narrow-beam side lighting: description

Apertural Size and Shape

15) Peristome height (PH), to 0.1 mm
16) Peristome width (PW), to 0.1 mm
17) Peristome height/width, to 0.1
18) Peristome width/shell diameter, to 0.1
19) Apertural lip width (LW), to 0.01 mm
20) Apertural lip width/peristome width, to 0.01

Apertural Barriers

21) Parietal tooth (P) size (minute, small, moderate, large, or massive) and whether notched or bifid
22) Palatal tooth (L) presence/absence, size (minute, small, moderate, large, or massive), and shape (description)
23) Parieto-palatal embayment (E) size: narrow, moderately wide, or wide
24) Columellar recessed baffle (RB) (= submerged columellar fold or lobe of Pilsbry, 1919) size (minute, small, moderate, large, or massive) and shape (rounded, nubbed, or pointed and tooth-like), and whether bifid
25) Baso-columellar lamella (BL) (none, weak, moderate, strong, very strong) and whether recessed
26) Baso-columellar tooth (BC): none, weak, small, moderate, large
27) Mid-columellar tooth (C) presence/absence, size (weak, small, moderate, large), and shape (description)
28) Upper-columellar tooth (UC) presence/absence, size (weak, small, moderate, large), and shape (description)
29) Baso-central tooth (B): (none, small, moderate, large) and whether recessed and concomitantly displaced toward the columella

Umbilicus

30) Umbilicus: description

al barriers and/or shell sculpture or shell shape, also differed in both initial-whorl size (diameter of the first 1.5 whorls, 1%-13% minimum difference) and shell coiling tightness (whorls/ln height, 2%-16% minimum difference). The 7 pairs with indistinguishable apertural barriers and shell sculpture (Table 2) were diagnosed by their combinations of initial-whorl size (8%-30% minimum difference) and shell coiling tightness (0%-18% minimum difference).

Table 3 shows character variation in 11 of the most variable species, and the illustrations (Figs. 2-103) show some additional variant specimens not included in Table 3. Shell height can vary 40% or more within a species, depending primarily on the number of whorls achieved before maturity. Height/diameter varies up to 35%, apical angle 40%, sutural-depth and barreling indices 180% and 200% or more, embryonic whorl-count 17%, peristome height/width 33%, peristome width/shell diameter 40%, and lip width/peristome width 155%. The umbilicus can vary from imperforate to a crevice, and from a crevice to a very narrow well. Because of the great variabilities of these characters, I used them sparingly and cautiously, if at all, in diagnosing species.

Primary diagnostics among species were, in approximate descending order of importance, apertural barriers, body-whorl sculpture, initial-whorl size, shell coiling tightness, embryonic sculpture, apertural shape (when extreme); and sutural crenulation. Each apertural barrier can vary somewhat in size and, to a lesser extent, in shape, but its presence/absence, disposition, and size and shape relative to other barriers, are fairly constant within a species (Table 3). Rare presence/absence exceptions all involve the baso-columellar tooth: *Gulella zanahary*i sp. nov. (Figs. 29, 69, 70), *G. fischerpiettei* sp. nov. (Figs. 32, 33), *G. satisfacta* (Figs. 34-38), and *G. ambalaniranae* (Figs. 71-74). Rare fixed-position exceptions involve the baso-central tooth's variable depth of recess, which, as I have interpreted it, may (Figs. 89-92) or may not (Figs. 76-78) correlate with displacement toward the columella.

Shell sculpture as seen in apertural view on the body and penultimate whorls, appears relatively stable within a species (Table 3). Sutural crenulation, although apparently independent of rib-sculpture in *Gulella* as it is in *Parvedentulina* Emberton and Pearce, 2000 (Emberton, in press b), sometimes produces faint subsutural impressions that I have discounted as rib sculpture. All species seem to show irregular growth lines, which I have ignored. Pre-apertural ribbing (Fischer-Piette *et al.*, 1994: figs. 60-62) seems ubiquitous within Madagascan *Gulella*, but I have not treated it here. Nor have I examined whether apical, post-embryonic ribbing differs from lower-whorl ribbing, except in the case of *Gulella ambanikelia* sp. nov., where the difference was extreme and unavoidably obvious.

The critical diagnostic roles of initial-whorl size (diameter of first 1.5 whorls) and shell coiling tightness (whorls/ln height) have already been demonstrated in Tables 2 and 4. In Table 3, within-species variation ranges about 1%-8% for both (up to 12% in subspeciated species). Thus, Table 3 reinforces my confidence in the stability and diagnostic value of these two indices.

Embryonic-shell sculpture can range from smooth to faintly ribbed or from smooth to a trace of sutural notches within a species. Other, more distinctive sculptures such as beaded or spirally grooved, however, seem consistent and diagnostic. Apertural shape in a few extreme cases was clearly diagnostic. I have also occasionally drawn on sutural crenulation for diagnosing both subspecies and species, as its variance seems relatively low (Table 3).

Table 4 compares subspecies or possible subspecies within six extremely variable species. Four of these species have what I deemed morphologically distinct subspecies that seem well isolated by uninhabitable savannah (*Gulella ambrensis* sp. nov., *G. benjamini* sp. nov.) or by impassable karstic ridges within Ankarana Reserve (*G. fischerpiettei* sp. nov., *G. satisfacta*). The other two species I did not divide into subspecies. The broad range of *G. antongilae* sp. nov. was recently continuous rainforest, and its aberrant shells from Soanierana-Ivongo may have resulted from abnormal growth conditions in exotic eucalypt forest and scrub. The aberrant Namoroka population of *G. vakinifia* sp. nov. could be due to character displacement by *G. celestinae* sp. nov.; variation of *G. vakinifia* sp. nov. within Bemaraha Reserve is nearly covered by its variation within the far-distant Namoroka Reserve, although the tightly and loosely coiled shells respectively of southern and northern Bemaraha, separated by the Beboka River, could possibly be subspecies.

KEY TO SPECIES AND SUBSPECIES

References are to published figures; see the Systematics section below for authors and dates of species.

1a. Apertural dentition limited to a small parietal tooth, coiling very loose (whorls/ln height 2.1-3.0) 2

1b. Apertural dentition of two or more teeth, coiling loose to very tight (whorls/ln height 3.1-5.4). 3

2a. Apex rounded, aperture wide, coiling looser (whorls/ln height 2.1) . . . . . .*G. microdon* Fischer-Piette *et al.* (1994): fig. 52

2b. Apex angular, aperture narrow, coiling tighter (whorls/ln height 3.0) . . . . . *G. rubinsterni* Fischer-Piette *et al.* (1994): fig. 53

3a. Apertural dentition of parietal and palatal teeth only

Table 2. Coiling tightness, initial-whorl size, and other differences between similar pairs of species in sympatry and allopatry. Abbreviations: *ambr., ambrensis*; BCT, baso-columellar tooth present; CRBM, columellar recessed baffle massive; MnDiff, minimum difference between sympatric species; MWC, middle whorls constricted; PABAP, pre-apertural base angular in profile; PTIO, palatal tooth often with internal outlier; RCD, ribbing completely diminished between upper and lower sutures; RU, ribbing undiminished between upper and lower sutures; *sat., satisfacta*; #Sn, number of snails; #Sta, number of stations; UCTP, upper-columellar tooth present; WRA, whorls ribbed above.

				Whorls/ln(Height)		Diam 1st 1.5 Whorls		
Sp./ssp.	Station(s)	#Sta	#Sn	Range	MnDiff	Range	MnDiff	Other Diagnostics
masoalae	306,307,311,314[1]	4	7	3.28-3.35[3]		1.25-1.35		–
antongilae	295,300,303[2]	3	3	3.38-3.50[4]	1%	1.10-1.13	10%	–
antongilae	364,366,756,758	4	4	3.42-3.58		1.05-1.11		–
boucheti	218	1	1	3.57		1.36		–
boucheti	222	1	1	3.82	12%	1.35	13%	–
petitboucheti	223[5]	1	1	4.34		1.18		–
ankaranensis	554,564,570,571	4	4	4.89-5.07		0.75- 0.79		–
ankaranensis	558	1	4	5.02-5.12	5%	0.75- 0.79	8%	–
f. fischerpiettei	558	1	4	4.69-4.78		0.86- 0.90		–
f. fischerpiettei	803	1	1	4.59		0.88		–
ankaranensis	554,558,564,572	1	1	4.96-5.12		0.75- 0.79		–
ankaranensis	571	1	1	4.89	12%	0.78	18%	–
sat. charlesblanci	571	1	1	4.30		0.95		–
ankaranensis	554,558,570,571	4	6	4.89-5.12		0.75- 0.79		–
ankaranensis	564	1	1	5.07	18%	0.78	17%	–
sat. satisfacta	564	1	4	4.09-4.18		0.94- 0.95		–
sat. satisfacta	576,577	2	5	4.12-4.21		0.912-0.962		–
mahia	400	1	2	4.09-4.12		0.99 -1.025		–
mahia	239	1	1	4.07	4%	0.975	4%	–
ranomasina	239	1	2	4.22-4.26		0.925-0.932		MWC
ranomasina	238,240,241	3	7	4.28-4.40		0.875-0.925		MWC
mahia	400	1	2	4.09-4.12		0.99 -1.025		–
mahia	239	1	1	4.07	4%	0.975	11%	–
ambr. capdambri	238	1	1	3.92		1.100		–
ambr. capdambri	230,233	2	3	3.77-3.90		1.058-1.075		–
ambr. capdambri	230,233	2	3	3.77-3.90		1.058-1.075		–
ambr. capdambri	238	1	1	3.92	8%	1.100	13%	–
zanaharyi	238	1	1	4.28		0.962		CRBM,PABAP,PTIO
zanaharyi	239,241,400,404,407	5	10	3.93-4.15		0.975-1.025		CRBM,PABAP,PTIO
ambr. orangea	224	1	3	3.88-4.04		1.025-1.038		–
capmini	224	1	3	4.33-4.63	7%	0.950-1.000	2%	WRA
ambr. orangea	225	1	1	3.97		1.03		–
capmini	225	1	1	4.33	8%	1.08	5%	WRA
jaominai	401	1	1	3.94		0.938		–
jaominai	404	1	2	3.90-3.98	2%	0.912-0.925	6%	–
zanaharyi	404	1	2	4.06-4.08		0.988		CRBM,PABAP,PTIO
zanaharyi	238,239,241,400,407	5	9	3.93-4.28		0.962-1.025		CRBM,PABAP,PTIO
jaominai	401	1	1	3.94		0.938		–
gallorum	401	1	3	3.71-3.80	4%	1.225-1.312	23%	–
jaominai	404	1	2	3.90-3.98		0.912-0.925		–
gallorum	405[6]	1	2	3.82-3.90	0%	1.325	30%	–
marojejyae	649	1	1	3.34		1.16		RCD
michellae	649	1	1	3.96	16%	1.14	2%	RU,BCT
vakinifia	61,62,64	3	7	4.66-4.82		0.782-0.838		ribbed
vakinifia	74	1	2	4.93-5.01	2%	0.838-0.850	1%	ribbed
celestinae	74	1	6	4.67-4.81		0.818-0.842		smooth,UCTP

[1] juveniles also found at 294, 295, and 297. [2] also found at 283, 285, 294, 295, and 297. [3] n = 3. [4] n = 2. [5] also occurs at 222, where shell is virtually identical. [6] upslope from and only 20 m higher elevation than 404.

Table 3. Character variation within 11 especially variable species of Madagascan *Gulella*, based on extreme individuals. Characters as in Fig. 1 and in Table 1. Abbreviations: D1st1.5Wh, diameter of first 1.5 whorls (mm); EmbWhls, embryonic whorl count; *fischerp., fischerpiettei*; fRibs, faint riblets; fSpiral, faint spiral grooves or striae; LipW/PsW, apertural-lip width/peristome width; m-l, moderate to large; massi, massive; md-lg, moderate to large; p-t, peg-like to triangular; pegTr-rdTr, peg-triangular to rounded-triangular; PsHt/Wdth, peristome height/width; PsW/ShD, peristome width/shell diameter; r-t, rounded to triangular; rct-rt, rectangular to rounded-triangular; rd-knTr, rounded to knobbed-triangular; rnd, rounded; sm, smooth; sNt, slightly notched; T, tooth; trStNt, smooth to trace of sutural notches; vStrong, very strong; Wh/lnHt, number of whorls divided by natural log of shell height (index of coiling tightness).

Species	n	Height	Ht/Diam	Whorls	Wh/lnHt	ApAngle	Barrel	SutDepth	SutCrenul
*ambrensis**	5*	5.8-6.8	2.1-2.5	6.5-7.4	3.7-4.0*	90-115	3.5-05.0	4.0-9.0	weak-strong*
antongilae	3	5.9-7.2	2.2-2.6	6.2-6.8	3.4-3.5	85-095	< 0-03.5	4.9-7.7	moderate
*benjamini**	3*	3.0-3.4	1.9-2.1	5.8-6.0	4.8-5.4*	85-100	2.5-03.4	5.6-9.8	weak
bobaombiae	3	4.0-4.2	2.5-2.7	6.8-7.2	4.9-5.1	85-115	< 0-03.6	3.9-5.8	strong
boucheti	2	5.7-7.5	2.1-2.6	6.2-7.7	3.6-3.8	95-120	7.0-09.1	1.2-1.8	strong
capmini	2	4.8	1.9-2.0	6.8-6.9	4.3	120	0.0-2.63	3.7-6.6	moderate
*fischerp.**	2*	4.0-4.7	2.3-2.6	6.4-7.3	4.6-4.7*	90-115	1.1-3.3	3.3-5.6	moderate
hafahafa	2	6.9-7.7	1.7-2.3	6.6-7.6	3.4-3.7	80-095	0.9-07.4	4.8-7.3	moderate
*satisfacta**	4*	4.7-5.8	2.4-2.8	6.7-7.2	4.1-4.3*	85-105	0-4.2	1.5-8.5	mod-strong*
vakinifia	3	3.5-4.9	2.1-2.8	6.2-7.6	4.6-5.0	80-085	2.2-05.8	4.6-7.7	strong
zanaharyi	2	5.3-6.9	2.2-2.7	6.7-8.3	4.0-4.3	100-105	2.4-5.1	1.3-3.6	moderate

Species	RibStrength	RibDimin	EmbWhls	D1st1.5Wh	EmbSculpt	PsHt/Wdth
*ambrensis**	none	–	1.8-2.1	1.03-1.17*	sm-trStNt	1.0-1.1
antongilae	none	–	1.9-2.0	1.08-1.11	smooth	1.0-1.2
benjamini	moderate	none	1.8-2.1	0.73-0.79	sm-fRibs	1.0
bobaombiae	none	–	2.0-2.2	0.74-0.79	smooth	1.0-1.1
boucheti	none	–	1.6-1.7	1.35-1.36	fSpiral	1.0-1.1
capmini	moderate	complete	2.1-2.2	1.00-1.08	smooth	0.8-0.9
*fischerp.**	none	–	1.9-2.0	0.80-0.90*	smooth	1.0
hafahafa	strong	none	2.1	1.00-1.03	beaded	1.2
*satisfacta**	none-weak*	none	2.1	0.91-0.95	smooth	0.9-1.2
vakinifia	strong	none	1.8-2.1	0.78-0.80	sm-fRibs	1.1-1.4
zanaharyi	none	–	1.8-2.0	0.93-0.99	smooth	1.0-1.1

Species	PsW/ShD	LipW/PsW	ParietalT	PalatalTooth	Par-PalEmbayment
*ambrensis**	0.7	0.14-0.22	large-mod*	large, triang	mod wide
antongilae	0.6	0.11-0.14	small	sm-md, rct-rt	wide
benjamini	0.6-0.7	0.17-0.20	moderate	md-lg, tr-pegTr	wide
bobaombiae	0.7-0.8	0.19-0.26	large	lg, triang-pegTr	mod wide
boucheti	0.7	0.18-0.21	moderate	md, rnd-squared	mod wide
capmini	0.7	0.15-0.19	moderate	large, rd-knTr	mod wide
*fischerp.**	0.7	0.16-0.23	large-mod*	large, triang	mod wide
hafahafa	0.5-0.7	0.24-0.34	lg-massi	lg-massi, bifid	narrow-mod wide
*satisfacta**	0.7	0.16-0.23	large	lg, pegTr-rdTr	mod wide
vakinifia	0.6-0.7	0.11-0.28	massi, sNt	massive, bifid	narrow
zanaharyi	0.6-0.7	0.20	lg-massive	lg-vLg, triang	fairly narrow

Species	Baso-CentT	Baso-ColLamella	Baso-ColT	Mid-ColT	Upp-ColT	ColRecBaffle
*ambrensis**	none	strong	none	none	none	moderate
antongilae	none	none	none	none	none	minute
benjamini	none	none	none	m-l, r-t	none	small
bobaombiae	none	moderate	small-mod	none	none	moderate
boucheti	none	none	none	none	none	minute
capmini	none	strong	none	none	none	moderate
*fischerp.**	none	moderate	no-weak*	none	none	small-modera*
hafahafa	small-mod	none	none	m-l, p-t	peg-like	small
*satisfacta**	none	strong-vStrong*	none	wk-none*	none	small
vakinifia	small-lg	moderate	none	m-l, rnd	none	moderate
zanaharyi	none	mod-stg, recess	none-mod	none	none	massive

Species	Umbilicus	Species	Umbilicus
*ambrensis**	crevice	*fischerp.**	imperf-crevice
antongilae	imperf-crevice	*hafahafa*	crevice-very narrow well
benjamini	crevice	*satisfacta**	imperf-crevice
bobaombiae	tiny crevice	*vakinifia*	crevice-very narrow well
boucheti	imperf-minute crevice	*zanaharyi*	small crevice
capmini	crevice		

*divided into subspecies (see Table 4).

(although the columellar recessed baffle can resemble a tooth) 4

3b. Apertural dentition of parietal and palatal teeth and at least one other tooth 51

4a. Parietal and palatal teeth minute and approximately equal in size, shell height less than 4.5 mm (whorls/ln height 4.5), moderately strong rib sculpturing . . . . . *G. nifikelia* Fig. 2

4b. Parietal and palatal teeth small to large and generally unequal in size, if small and approximately equal then shell height is greater than 6.5 mm (whorls/ln height 3.4) and rib sculpture is very weak 5

5a. Coiling loose (whorls/ln height 3.1-3.5), shell sculpture smooth or nearly so (but with a crenulate suture), parietal tooth small, parieto-palatal embayment wide. 6

5b. Coiling moderate to tight (whorls/ln height 3.6-5.4), or, if loose (whorls/ln height 3.1-3.5), shell sculpture moderately to strongly ribbed, parietal tooth moderate to large, parieto-palatal embayment narrow to moderate in width 8

6a. Coiling looser (whorls/ln height 3.1), Antalaha region northeast of Masoala Peninsula . . . . . *G. bouchardi* Fischer-Piette *et al.* (1994): plate V fig. 1

6b. Coiling tighter (whorls/ln height 3.3-3.5), western Masoala Peninsula and southwest of it 7

7a. Diameter of first 1.5 whorls about 1.3 mm, coiling generally looser (whorls/ln height about 3.3-3.4), western Masoala Peninsula . . . . . *G. masoalae* Fig. 3

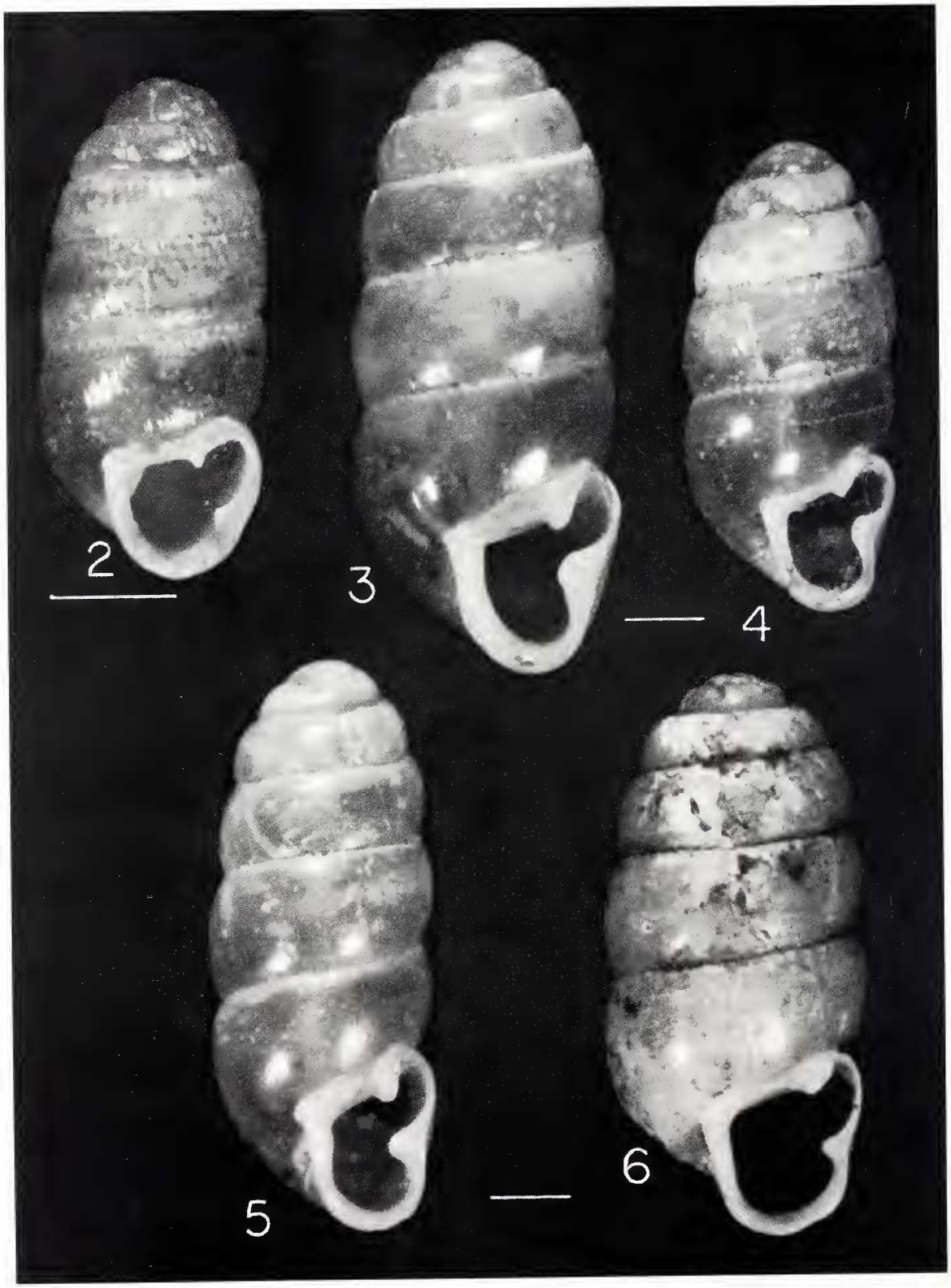
7b. Diameter of first 1.5 whorls about 1.1 mm, coiling generally tighter (whorls/ln height about 3.4-3.6), western Masoala Peninsula and southwest of it . . . . . *G. antongilae* Figs. 4, 5, 6

8a. Columellar recessed baffle only shallowly recessed and nubbed or bifid like a third tooth; shell cylindrical, smooth, without sutural crenulation; parietal tooth smallish and sometimes weakly bifid; palatal tooth smaller and shaped like a rounded nub or peg;

Table 4. Coiling tightness, initial-whorl size, and other differences among subspecies and possible subspecies. Abbreviations: ATVS, apertural teeth very small; BCLM, baso-columellar lamella massive and extending upward to near the columellar insertion; +c, sympatric with *Gulella celestinae*; -c, allopatric from *G. celestinae*; CWRS, continuous, weak rib sculpture; D1st1.5Wh, diameter of the first 1.5 whorls; DF, deciduous forest; EFS, eucalypt (exotic) forest and scrub; MCT, mid-columellar tooth present; PT+R, palatal tooth recessed to not recessed; PTLLE, palatal tooth lamellar all the way to the apertural-lip edge; PTLSBLE, palatal-tooth lamella stops before the apertural-lip edge; RF, rainforest; SCS, sutural crenulation strong; SCW, sutural crenulation weak; #Sn, number of snails; #Sta, number of stations; Wh/lnHt, shell whorls divided by the natural logarithm of shell height.

Species/Subspec.	Locality	#Sta	#Sn	Wh/lnHt	D1st1.5Wh	Other Differences
antongilae	W. Masoala	3	3	3.38-3.50[1]	1.10-1.13	RF
antongilae	Mananara	1	1	3.45	1.11	RF
antongilae	Ambatovaky	2	2	3.42-3.58	1.05- 1.06	RF
antongilae	Soanierana	2	3	3.38[2]	1.08- 1.18	EFS,ATVS
antongilae	IsleSteMarie	1	1	3.48	1.10	RF
f. fischerpiettei	Ankarana	2	5	4.59-4.78	0.86- 0.90	–
f. enigma	Ankarana	2	4	4.58-4.71	0.80- 0.84	–
s. satisfacta	Ankarana	3	9	4.09-4.21	0.913-0.962	–
s. charlesblanci	Ankarana	1	1	4.30	0.950	MCT
s. vitsia	Ankarana	1	1	4.18	0.950	CWRS,BCLM
a. ambrensis	Mt. d'Ambre	2	8	3.79-3.97	1.025-1.050	PTLSBLE,SCW,RF
a. andavakoerae	Andavakoera	2	2	3.68-3.90	1.075-1.100	PTLLE,SCS,DF
a. capdambri	Cap d'Ambre	2	4	3.77-3.92	1.058-1.100	PTLSBLE,SCS,PT+R,DF
a. orangea	Cap Mine	2	4	3.88-3.98	1.025-1.038	PTLSBLE,SCS,DF
a. rakotomalalai	Analamera	2	2	3.76-3.87	1.150-1.168	PTLLE,SCS,DF
b. benjamini	Vohimena Mts	2	2	4.8- 4.9	0.73- 0.79	–
b. saintelucensis	ForêtSteLuce	1	1	5.4	0.78	–
vakinifia	S. Bemaraha	1	4	4.99-5.13	0.775-0.838	–
vakinifia	N. Bemaraha	1	3	4.45-4.64	0.800-0.812	–
vakinifia	Namoroka -c	3	7	4.66-4.82	0.782-0.838	–
vakinifia	Namoroka +c	1	2	4.93-5.01	0.838-0.850	–

[1]n = 2. [2]n = 1.



Figs. 2-6. Fig. 2. *Gulella nifikelia* sp. nov. holotype, Manombo Reserve. Fig. 3. *G. masoalae* sp. nov. holotype, western Masoala Peninsula. Figs. 4-6. *G. antongilae* sp. nov.: Fig. 4 holotype, western Masoala Peninsula; Figs. 5, 6 paratypes: Fig 5 southwest of Mananara; Fig. 6 exotic eucalypt forest, Soanierana Ivongo. All scale bars 1 mm.

parietal-palatal embayment wide 9
8b. Otherwise 10

9a. Shell smaller for the same number of whorls (whorls/ln height about 3.9), diameter of first 1.5 whorls about 0.9 mm . . . . . *G. andreana* Fig. 7
9b. Shell larger for the same number of whorls (whorls/ln height about 3.6), diameter of first 1.5 whorls about 1.1 mm . . . . . *G. beandreana* Figs. 8, 9

10a. Parietal tooth deeply recessed, aperture constricted centrally into an hourglass shape . . . . . *G. constricta* Fig. 10
10b. Parietal tooth not recessed, aperture constricted slightly if at all 11

11a. Baso-columellar lamella absent to weak 12
11b. Baso-columellar lamella moderate to strong 30

12a. General rib sculpture weak to none 13
12b. General rib sculpture strong to moderate 24

13a. Aperture roughly triangular, parietal tooth bifid . . . . . *G. ambatovakiae* Fig. 12
13b. Aperture rounded to ovate, parietal tooth undivided 14

14a. Diameter of first 1.5 whorls about 1.5 mm, height generally greater than 11 mm . . . . . *G. magnifica* Fig. 11
14b. Diameter of first 1.5 whorls 1.3 mm or less, height less than 9.5 mm 15

15a. Rib sculpture weak but conspicuous, shell tall (height/diameter 2.8 or greater) and cylindrical to columnar 16
15b. Rib sculpture absent or weak and inconspicuous, shell stouter (height/diameter 2.6 or less) and barreled to slightly columnar 17

16a. Diameter of first 1.5 whorls 1.0-1.1 mm . . . . . *G. pseudandreana* Fig. 13
16b. Diameter of first 1.5 whorls 1.2-1.3 mm . . . . . *G. gallorum* Fig. 14

17a. Parietal and palatal teeth very large, columellar recessed baffle conspicuous . . . . . *G. rakotoarisoni* Fig. 15
17b. Parietal and palatal teeth moderate, columellar recessed baffle inconspicuous or not visible in apertural view 18

18a. Diameter of first 1.5 whorls 1.2-1.4 mm; palatal tooth low, broad, and squarish; sutures shallowly impressed; embryonic whorls 1.6 to 1.7 19
18b. Diameter of first 1.5 whorls 0.8-1.0 mm; palatal tooth elevated, narrow, and triangular or pegged; sutures moderately impressed; embryonic whorls 1.8 to 2.2 20

19a. Diameter of first 1.5 whorls about 1.4 mm; whorls descending more rapidly (whorls/ln height about 3.6-3.8) . . . . . *G. boucheti* Figs. 16, 17
19b. Diameter of first 1.5 whorls about 1.2 mm; whorls descending more slowly (whorls/ln height about 4.3) . . . . . *G. petitboucheti* Fig. 18

20a. Tighter coiling (whorls/ln height about 4.4-4.7) 21
20b. Looser coiling (whorls/ln height about 4.0-4.3). . . . 23

21a. Diameter of first 1.5 whorls about 0.95 mm; sutural crenulation weak; southeasternmost Madagascar . . . . . *G. reeae* Fig. 19
21b. Diameter of first 1.5 whorls about 0.80-0.81 mm; sutural crenulation strong; central to south-central Madagascar 22

22a. Looser coiling (whorls/ln height about 4.5); aperture proportionally smaller (aperture width/shell diameter 0.5); south-central eastern rainforest . . . . . *G. miaranoniae* Fig. 20
22b. Tighter coiling (whorls/ln height about 4.7); aperture proportionally larger (aperture width/shell diameter 0.7); central western semi-deciduous forest . . . . . *G. bebokae* Fig. 21

23a. Looser coiling (whorls/ln height about 4.0); diameter of first 1.5 whorls 0.9-1.0 mm; Manakara region (Fotobohitra) . . . . . *G. fotobohitrae* Fig. 22
23b. Tighter coiling (whorls/ln height about 4.2-4.3); diameter of first 1.5 whorls about 0.8 mm; Tamatave region (Betampona Reserve) . . . . . *G. razafyi* Fig. 23

24a. Shell height generally greater than 9 mm: looser coiling (whorls/ln height about 3.2-3.4) 25
24b. Shell height generally less than 7.5 mm: tighter coiling (whorls/ln height about 3.7-4.4) 26

25a. Looser coiling (whorls/ln height about 3.2), middle whorls with flattened peripheries . . . . . *G. josephinae* Fig. 24
25b. Tighter coiling (whorls/ln height about 3.4), middle whorls with rounded peripheries . . . . . *G. soulaiana* Fischer-Piette *et al.* (1994): plate IV fig. 19

Figs. 7-12. Fig. 7. *Gulella andreana* Fischer-Piette, Blanc and Vukadinovic, 1974, specimen, Ranomafana National Park. Figs. 8, 9. *G. beandreana* sp. nov.: Fig. 8 holotype, Manombo Reserve; Fig. 9 paratype, Mount Ambalanirana. Fig. 10. *G. constricta* sp. nov. holotype, Tsaratanana Reserve. Fig. 11. *G. magnifica* sp. nov. holotype, Ankarana Reserve. Fig. 12. *G. ambatovakiae* sp. nov. holotype, Ambatovaky Reserve. All scale bars 1 mm.

26a. General rib sculpture very strong and high-standing; Ankarana Reserve and vicinity 27
26b. General rib sculpture moderately strong and low-standing; elsewhere than Ankarana Reserve 28

27a. Looser coiling (whorls/ln height about 3.7); larger initial whorl (diameter of first 1.5 whorls about 1.0 mm) . . . . . *G. rugosa* Fig. 25
27b. Tighter coiling (whorls/ln height about 4.1); smaller initial whorl (diameter of first 1.5 whorls about 0.8 mm) . . . . . *G. columna* Fig. 26

28a. Palatal tooth high in position and notched opposite the parietal tooth; tighter coiling (whorls/ln height 4.5-4.6). . . . . *G. pearcei* Fig. 27
28b. Palatal tooth medial in position and unnotched; looser coiling (whorls/ln height 4.1-4.4). 29

29a. Looser coiling (whorls/ln height about 4.1); rainforest in north-central Madagascar . . . . . *G. tsaratananae* Fig. 28
29b. Tighter coiling (whorls/ln height about 4.4); dry forest in southwestern Madagascar . . . . . *G. miaryi* Fischer-Piette *et al.* (1994): fig. 54

30a. General rib sculpture weak to none 31
30b. General rib sculpture strong to moderate 46

31a. Columellar recessed baffle huge, pre-apertural base angular in profile, palatal tooth massive and often with deeply internal outlier . . . . . *G. zanaharyi* Figs. 29, 69, 70
31b. Columellar recessed baffle small to moderate, pre-apertural base rounded in profile, palatal tooth moderate to large and without a deeply internal outlier 32

32a. Diameter of first 1.5 whorls about 1.3 mm; palatal tooth transverse; parietal tooth joined to and continuous with the apertural lip . . . . . *G. lohabea* Fig. 30
32b. Diameter of first 1.5 whorls about 0.8-1.1 mm; palatal tooth spirally lamellar to nodular; parietal tooth generally disjunct from and not continuous with the apertural lip. 33

33a. Tighter coiling (whorls/ln height 4.6-5.2) 34
33b. Looser coiling (whorls/ln height 3.7-4.4) 36

34a. Very tight coiling (whorls/ln height 5.0-5.2); diameter of first 1.5 whorls 0.75-0.79 mm . . . . . *G. ankaranensis* Fig. 31
34b. Looser coiling (whorls/ln height 4.6-4.8); diameter of first 1.5 whorls 0.80-0.90 mm 35

35a. Diameter of first 1.5 whorls 0.86-0.90 mm; palatal tooth nub-like and slightly recessed; parietal tooth separated by a groove from the apertural lip . . . . . *G. fischerpiettei s.s.* Fig. 32
35b. Diameter of first 1.5 whorls 0.80-0.84 mm; palatal tooth spirally lamellar and not recessed; parietal tooth continuous with the apertural lip . . . . . *G. fischerpiettei enigma* Fig. 33

36a. Diameter of first 1.5 whorls 0.88-1.00 mm (rarely to 1.02 mm); whorls/ln height 3.90-4.40 37
36b. Diameter of first 1.5 whorls 1.02-1.17 mm; whorls/ln height 3.68-3.98 42

37a. Columellar recessed baffle broadly rounded and not like a tooth; Ankarana Reserve 38
37b. Columellar recessed baffle nubbed and toothlike; southern Cap d'Ambre 40

38a. Whorls/ln height 4.3; small baso-columellar tooth present . . . . . *G. satisfacta charlesblanci* Fig. 34
38b. Whorls/ln height 4.1-4.2; no baso-columellar tooth 39

39a. Whorls covered with weak rib sculpture; baso-columellar lamella massive and extending upward to near the columellar insertion . . . . . *G. satisfacta vitsia* Fig. 35
39b. Whorls smooth; baso-columellar lamella strong but not approaching the columellar insertion . . . . . *G. satisfacta satisfacta* Figs. 36, 37, 38

40a. Diameter of first 1.5 whorls 0.98-1.02 mm; whorls/ln height 4.1 . . . . . *G. mahia* Figs. 39, 40
40b. Diameter of first 1.5 whorls 0.88-0.93 mm; whorls/ln height either 4.2-4.4 or 3.9-4.0 41

41a. Whorls/ln height 4.2-4.4; sides of shell concave . . . . . *G. ranomasina* Fig. 41
41b. Whorls/ln height 3.9-4.0; sides of shell convex to straight . . . . . *G. jaominai* Fig. 42

42a. Weak sutural crenulation; Montagne d'Ambre rain forest . . . . . *G. ambrensis s.s.* Fig. 43
42b. Strong sutural crenulation; deciduous forest elsewhere 43

43a. Palatal-tooth lamella extends all the way to the apertural-lip edge; latitudes south of Diego Suarez . . . 44
43b. Palatal-tooth lamella stops before the apertural-lip edge; latitudes north of Diego Suarez 45

44a. Diameter of first 1.5 whorls 1.075-1.100 mm; Andavakoera massif . . . . . .

Figs. 13-18. Fig. 13. *Gulella pseudandreana* sp. nov. holotype, Bemaraha Reserve. Fig. 14. *G. gallorum* Fischer-Piette, Blanc and Salvat, 1975, specimen, Cap d'Ambre. Fig. 15. *G. rakotoarisoni* sp. nov. holotype, Ankarana Reserve. Figs. 16, 17. *G. boucheti* Fischer-Piette, Blanc, Blanc and Salvat, 1994, specimens: Fig. 16 type locality, Montagne des Français; Fig. 17 Montagne des Orchides. Fig. 18. *G. petitboucheti* sp. nov. holotype, Montagne des Français. All scale bars 1 mm.

. . . . . .*G. ambrensis andavakoerae* Fig. 44

44b. Diameter of first 1.5 whorls 1.150-1.168; Analamera Reserve . . . . . .*G. ambrensis rakotomalalai* Fig. 45

45a. Diameter of first 1.5 whorls 1.058-1.100 mm; palatal tooth often moderately recessed; Cap d'Ambre . . . . . *G. ambrensis capdambri* Fig. 46

45b. Diameter of first 1.5 whorls 1.025-1.038 mm; palatal tooth never recessed; Forêt d'Orange, Cap Mine . . . . . *G. ambrensis orangea* Fig. 47

46a. General rib sculpture continuing undiminished from upper to lower suture 47

46b. General rib sculpture strong at and below the upper suture but diminishing conspicuously toward the lower suture 48

47a. Palatal tooth transverse and squarish; looser coiling (whorls/ln height about 3.65); smaller initial whorl (diameter of first 1.5 whorls about 1.2 mm) . . . . . *G. bemarahae* Fig. 49

47b. Palatal tooth a short spiral lamella that is triangular in apertural view; tighter coiling (whorls/ln height about 3.85); larger initial whorl (diameter of first 1.5 whorls about 1.3 mm) . . . . . *G. nakamaroa* Fig. 50

48a. Columellar recessed baffle conspicuous, nubbed, and toothlike; palatal tooth recessed about as deeply as the recessed columellar baffle . . . . . *G. capmini* Figs. 48, 51

48b. Columellar recessed baffle inconspicuous, broadly rounded, not toothlike; palatal tooth much shallower than the recessed columellar baffle 49

49a. Shell large and loosely coiled (whorls/ln height about 3.3-3.4, diameter of first 1.5 whorls 1.0-1.1 mm) . . . . . .*G. marojejyae* Fig. 52

49b. Shell small and tightly coiled (whorls/ln height about 4.1-4.6, diameter of first 1.5 whorls 0.8-0.9 mm) 50

50a. Loose coiling (whorls/ln height about 4.1-4.2); large parietal tooth; deciduous-forest habitat . . . . . *G. griffithsi* Fig. 53

50b. Tight coiling (whorls/ln height about 4.5-4.6); small parietal tooth; rainforest habitat . . . . . *G. tsara* Fig. 54

51a. General rib sculpture extremely dense . . . . . *G. microstriata* Fig. 55

51b. General rib sculpture, when present, moderately dense 52

52a. General rib sculpture weak to none 53

52b. General rib sculpture strong to moderate 67

53a. Shell extremely minute (whorls/ln height about 5.4); no evident sutural crenulation . . . . *G. kelibea* Fig. 56

53b. Shell larger (whorls/ln height about 3.6-5.0); moderate to strong sutural crenulation 54

54a. Shell shape steeply pyramidal; whorls/ln height about 3.6; an introduced species found only in gardens and settlements . . . . . .*G. bicolor* Fischer-Piette *et al.* (1994): fig. 50

54b. Shell shape barreled to columnar; whorls/ln height about 3.7-5.0; native species not known from gardens or settlements 55

55a. Loose coiling (whorls/ln height about 3.7-3.8); initial whorl generally larger (diameter of first 1.5 whorls 1.0-1.2 mm) 56

55b. Tight coiling (whorls/ln height about 4.0-5.0); initial whorl generally smaller (diameter of first 1.5 whorls 0.8-1.0 mm) 57

56a. Narrow baso-columellar tooth; upper-columellar tooth often present; tighter coiling (whorls/ln height about 3.8); smaller initial whorl (diameter of first 1.5 whorls about 1.0-1.1 mm) . . . *G. analamerae* Fig. 57

56b. Broad baso-columellar tooth; never an upper-columellar tooth; looser coiling (whorls/ln height about 3.7); larger initial whorl (diameter of first 1.5 whorls about 1.2 mm) . . . . . *G. voliimarae* Fig. 58

57a. Mid-columellar tooth present, baso-columellar tooth absent (but its position may be approached by the mid-columellar tooth). 58

57b. Baso-columellar tooth present, mid-columellar tooth absent 60

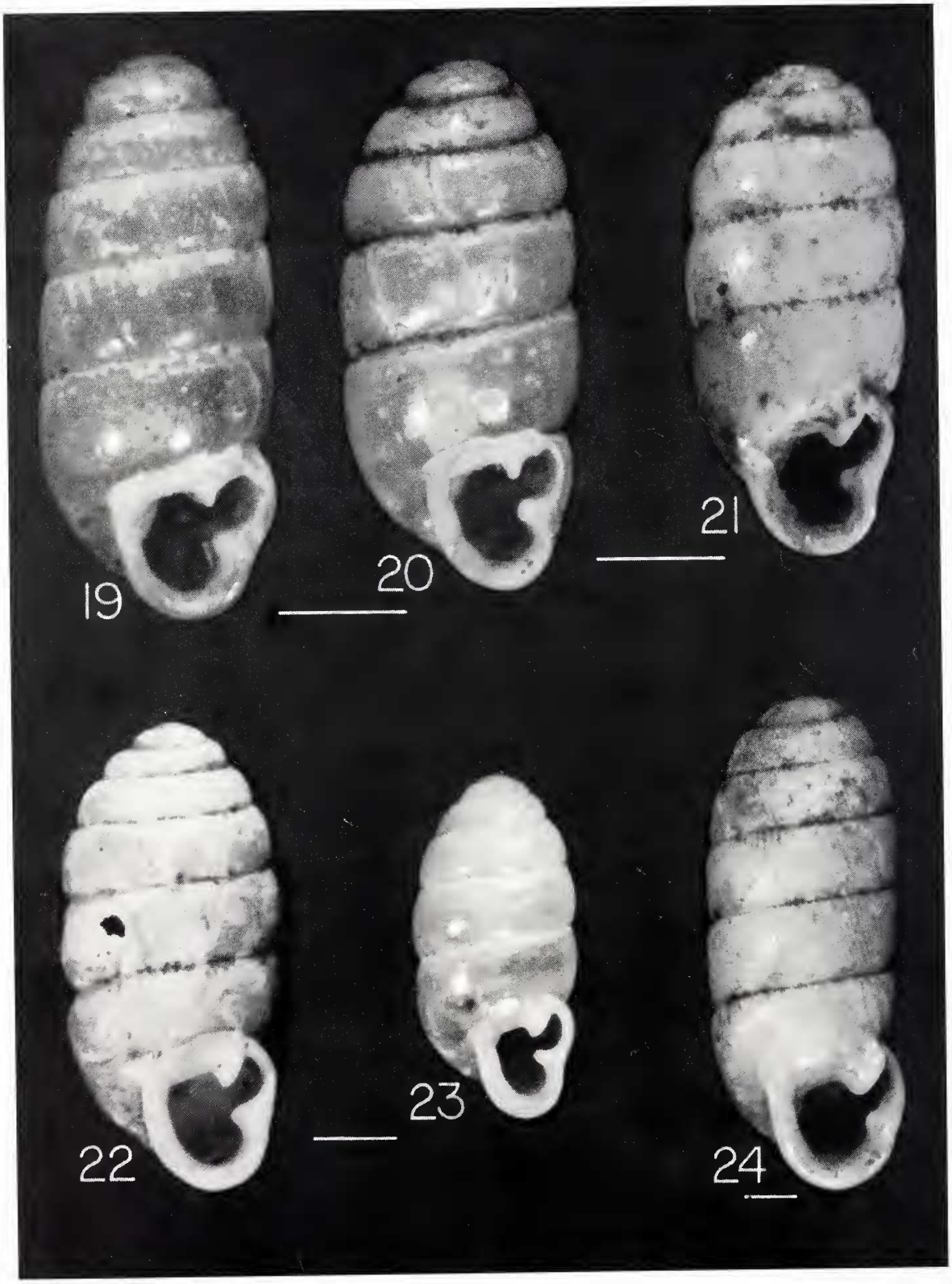
58a. Shell stout and loosely coiled (whorls/ln height about 4.3, diameter of first 1.5 whorls about 0.9); outer edge of peristome not conspicuously constricted . . . . . *G. nosybei* Fig. 61

58b. Shell slender and tightly coiled (whorls/ln height about 4.7-4.8, diameter of first 1.5 whorls about 0.8); outer edge of peristome conspicuously constricted 59

59a. No upper-columellar tooth; parietal and palatal teeth not conspicuously bifid . . . . . *G. tendronia* Fig. 59

59b. Upper-columellar tooth present; parietal and palatal teeth conspicuously bifid. . . . . *G. celestinae* Fig. 60

60a. Palatal and columellar sides of the peristome straight,



Figs. 19-24. Fig. 19. *Gulella reeae* Emberton and Pearce, 2000, holotype, south of Andohahela Reserve. Fig. 20. *G. miaranoniae* sp. nov. holotype, eastern Ranomafana National Park. Fig. 21. *G. bebokae* sp. nov. holotype, Bemaraha Reserve. Fig. 22. *G. fotobohitrae* sp. nov. holotype, east of Ranomafana National Park. Fig. 23. *G. razafyi* sp. nov. holotype, Betampona Reserve. Fig. 24. *G. josephinae* sp. nov. holotype, Namoroka Reserve. All scale bars 1 mm.

parallel, and slanted conspicuously inward toward the columella; whorls/ln height 4.4-4.5 and apical, post-embryonic whorls smooth 61

60b. Palatal and columellar sides of the peristome curved, non-parallel, and not slanted conspicuously inward; if whorls/ln height 4.4-4.5, then apical, post-embryonic whorls ribbed 62

61a. Palatal tooth notched to receive the parietal tooth and inwardly slanting downward; northern Cap d'Ambre . . . . . *G. bemoka* Fig. 62

61b. Palatal tooth unnotched and not inwardly slanting downward; Analamera Reserve . . . . . *G. vavakelia* Fig. 63

62a. Baso-columellar tooth large and buttressed more strongly above than below, palatal tooth slightly bifid . . . . . *G. mitsikia* Fig. 64

62b. Baso-columellar tooth moderate and buttressed equally above and below, palatal tooth undivided 63

63a. Shell small and tightly coiled (whorls/ln height 4.9-5.1, diameter of first 1.5 whorls 0.7-0.8 mm) . . . . . *G. bobaombiae* Figs. 65-67

63b. Shell larger and more loosely coiled (whorls/ln height 4.0-4.4, diameter of first 1.5 whorls 0.9-1.0 mm) 64

64a. Apical, post-embryonic whorls weakly but quite noticeably ribbed; baso-columellar tooth a distinct knob . . . . . *G. ambanikelia* Fig. 68

64b. Apical, post-embryonic whorls without noticeable rib sculpture; baso-columellar tooth broad and less distinct 65

65a. Columellar recessed baffle huge, pre-apertural base angular in profile, palatal tooth massive and often with deeply internal outlier; Cap d'Ambre . . . . . *G. zanaharyi* Figs. 29, 69, 70

65b. Columellar recessed baffle small to moderate, pre-apertural base rounded in profile, palatal tooth moderate to large and without a deeply internal outlier; Ankarana Reserve. 66

66a. Tight coiling (whorls/ln height 4.6-4.8) . . . . . *G. fischerpiettei* Figs. 32, 33

66b. Loose coiling (whorls/ln height 4.1-4.3) . . . . . *G. satisfacta* Figs. 34-38

67a. General rib sculpture diminishing almost completely toward the lower suture 68

67b. General rib sculpture diminishing little to none toward the lower suture 70

68a. Palatal tooth undivided and unnotched; shell large and loosely coiled (whorls/ln height about 3.8-3.9); baso-columellar tooth broad and indefinite . . . . . *G. ambalaniranae* Figs. 71-74

68b. Palatal tooth bifid or notched; shell smaller and more tightly coiled (whorls/ln height about 4.2-4.9); baso-columellar tooth narrower and clearly defined. . . . 69

69a. No mid-columellar or baso-central tooth; baso-columellar tooth small; palatal tooth bifid and not interlocking with the parietal tooth; shell smaller and more tightly coiled (whorls/ln height about 4.9) . . . . . *G. namorokae* Fig. 75

69b. Mid-columellar and baso-central teeth present and massive; no baso-columellar tooth; parietal and palatal teeth notched and interlocking; shell much larger and more loosely coiled (whorls/ln height about 4.2) . . . . . *G. mihomehia* Figs. 76-78

70a. Palatal tooth undivided and unnotched 71

70b. Palatal tooth bifid or with a secondary node 78

71a. No mid-columellar tooth; basal and columellar dentition limited to a single broad baso-columellar tooth 72

71b. Mid-columellar tooth present; baso-columellar tooth, if present, small and narrow 73

72a. Shell small and tightly coiled (whorls/ln height about 4.6-4.7, diameter of first 1.5 whorls about 0.75 mm); general rib sculpture strong; unique embryonic sculpture of minute riblets and two subsutural spiral grooves . . . . . *G. manomboae* Fig. 79

72b. Shell larger and more loosely coiled (whorls/ln height about 4.0, diameter of first 1.5 whorls about 1.15 mm); general rib sculpture moderate in strength; embryonic sculpture smooth . . . *G. michellae* Fig. 80

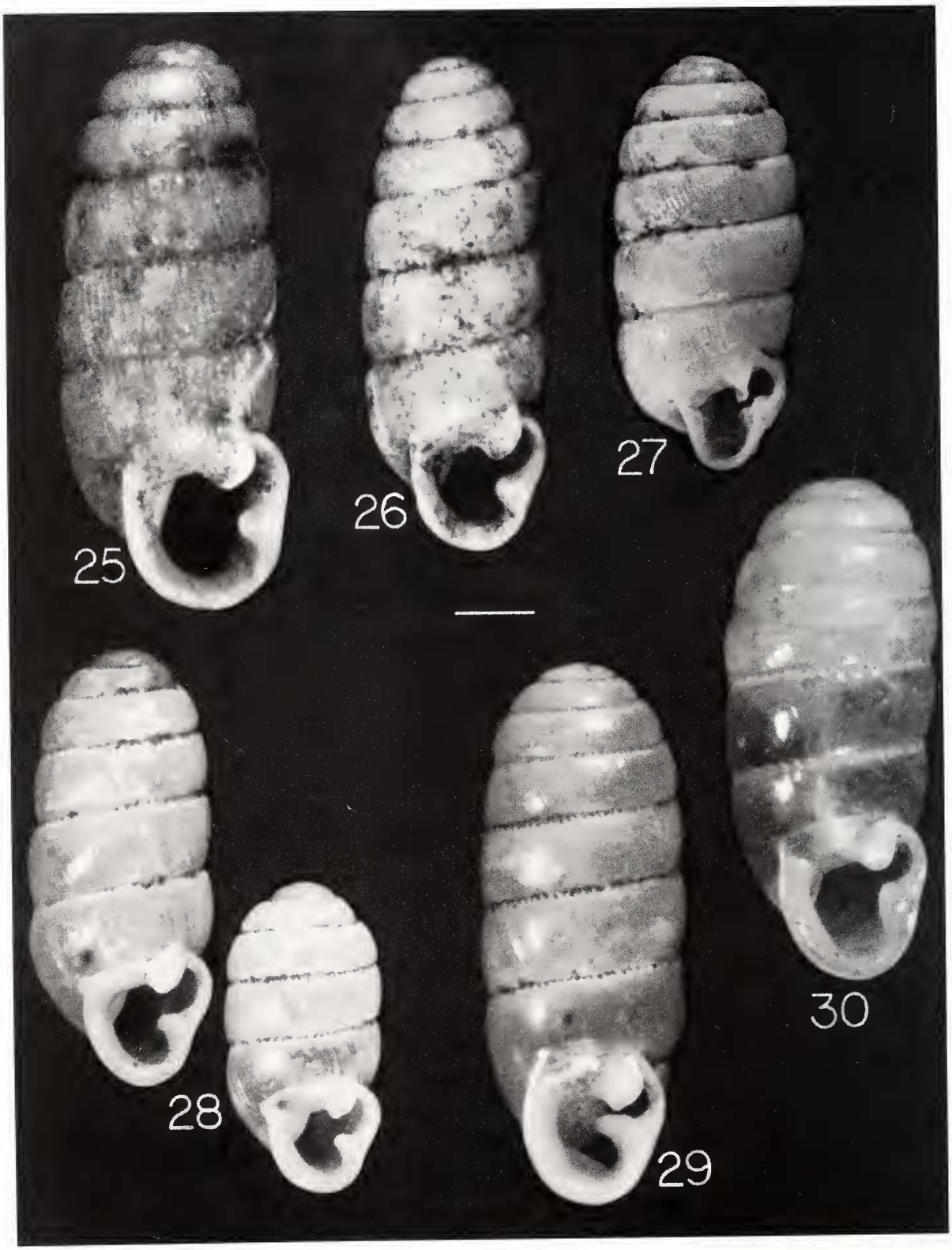
73a. Columellar recessed baffle enormous; baso-central and mid-columellar teeth both present; shell large and loosely coiled (whorls/ln height about 3.8) . . . . . *G. mahagaga* Fig. 81

73b. Columellar recessed baffle small to moderate; no baso-central tooth; shell smaller and more tightly coiled (whorls/ln height about 4.0-4.9) 74

74a. Shell small and tightly coiled (whorls/ln height 4.8-5.5) 75

74b. Shell large and loosely coiled (whorls/ln height about 4.0-4.1) 77

75a. Mid-columellar tooth connected at its base to both upper columellar and baso-columellar teeth; Marojejy Reserve (northeastern Madagascar). . . . . .



Figs. 25-30. Fig. 25. *Gulella rugosa* sp. nov. holotype, Ankarana Reserve. Fig. 26. *G. columna* sp. nov. holotype, Ankarana Reserve. Fig. 27. *G. pearcei* sp. nov. holotype, Montagne des Français. Fig. 28 (two shells). *G. tsaratananae* sp. nov.: larger shell holotype, smaller shell paratype, Tsaratanana Reserve. Fig. 29. *G. zanaharyi* sp. nov. holotype, northern Cap d'Ambre. Fig. 30. *G. lohabea* sp. nov. holotype, Analamera Reserve. Scale bar 1 mm.

. . . . . *G. hafa* Fig. 82

75b. Mid-columellar tooth isolated, no upper columellar or baso- columellar tooth present; extreme southeastern Madagascar 76

76a. Shell larger and more loosely coiled (whorls/ln height 4.8-4.9); montane forests . . . . . *G. benjamini s.s.* Figs. 83-84

76b. Shell smaller and more tightly coiled (whorls/ln height 5.4); coastal forests . . . . . *G. benjamini saintelucensis* Fig. 85

77a. Columella slanted conspicuously outward; palatal tooth smallish; near Andringitra Reserve (southeastern Madagascar). . . . . *G. lubeti* Fischer-Piette *et al.* (1994): fig. 63

77b. Columella nearly vertical; palatal tooth very large; Marojejy and Ambatovaky Reserves (northeastern Madagascar) . . . . . *G. mahafinaratra* Figs. 86-88

78a. Both upper- and mid-columellar teeth present; shell large and loosely coiled (whorls/ln height 3.4-3.7); unique, beaded embryonic sculpture . . . . . *G. hafahafa* Figs. 89-92

78b. Either upper- or mid-columellar tooth may be present, but not both; shell smaller and more tightly coiled (whorls/ln height 4.3-4.9); smooth to ribbed embryonic sculpture 79

79a. Strongly ribbed embryonic sculpture; palatal and mid-columellar teeth point directly to each other; no baso-central or baso-columellar tooth . . . . . *G. vatosoa* Fig. 93

79b. Smooth to trace-ribbed embryonic sculpture; palatal and mid-columellar teeth do not point directly to each other; a baso-central or baso-columellar tooth present 80

80a. Recessed baso-central tooth present; no baso-columellar tooth; parietal tooth slightly bifid and not entering directly into palatal-tooth notch . . . . . *G. vakinifia* Figs. 94-97

80b. No baso-central tooth; recessed baso-columellar tooth present; parietal tooth undivided and entering directly into palatal-tooth. 81

81a. Upper-columellar tooth present; shell coiling tighter (whorls/ln height about 4.4-4.5); Montagne des Orchides, southeast of Diego Suarez . . . . . *G. orchida* Figs. 98, 99

81b. No upper-columellar tooth; shell coiling looser (whorls/ln height about 4.2-4.3); southern Cap d'Ambre . . . . . *G. magnorchida* Fig. 100

SYSTEMATICS

Higher classification follows Nordsieck (1986). Type and voucher materials are placed in the Florida Museum of Natural History, University of Florida, Gainesville (UF); the Australian Museum, Sydney (AMS); the Academy of Natural Sciences of Philadelphia (ANSP); and the Muséum national d'Histoire naturelle, Paris (MNHN), which does not assign catalog numbers to its types.

Class GASTROPODA
Subclass PULMONATA
Order STYLOMMATOPHORA
Superfamily STREPTAXOIDEA
Family STREPTAXIDAE Gray, 1860
Genus *Gulella* Pfeiffer, 1856
(*sensu* Fischer-Piette *et al.*, 1994,
who separate *Gonospira* Swainson, 1840)

Gulella microdon (Morelet, 1860)
Fischer-Piette *et al.* (1994): fig. 52 (specimen)

DIAGNOSIS. One of only two Madagascan species of *Gulella* with the apertural dentition limited to a small parietal tooth; the other is *G. rubinsterni*. *G. microdon* differs from *G. rubinsterni* in its much looser coiling (whorls/ln height 2.1 vs. 3.0).

DESCRIPTION (based on illustration in Fischer-Piette *et al.*, 1994). Height 13.0 mm, diameter 6.2 mm (H/D 2.1), whorls 5.5 (whorls/ln height 2.14). Apical angle 125°, barreling 0.0%. Sutural depth 1.1%, sutural crenulation strong. In apertural view, penultimate and body whorls with moderate rib sculpture that diminishes completely, apparently, between upper and lower sutures. Peristome height 4.5 mm, width 4.8 mm (0.8 shell D; peristome H/W 0.9); apertural lip width 0.40 mm (0.09 peristome W). Apertural barriers consisting of a minute parietal tooth and a small columellar recessed baffle.

Gulella rubinsterni Fischer-Piette, Blanc,
Blanc and Salvat, 1994
Fischer-Piette *et al.* (1994): fig. 53 (holotype)

DIAGNOSIS. One of only two Madagascan species of *Gulella* with the apertural dentition limited to a small parietal tooth; the other is *G. microdon*. *G. rubinsterni* differs from *G. microdon* in its much tighter coiling (whorls/ln height 3.0 vs. 2.1).

DESCRIPTION OF HOLOTYPE (based on illustration in Fischer-Piette *et al.*, 1994). Height 15.0 mm, diameter 7.4 mm (H/D 2.0), whorls 8.0 (whorls/ln height 2.95). Apical angle 110°, barreling -2.5%. Sutural depth 6.1%. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and

Figs. 31-38. Fig. 31. *Gulella ankaranensis* Fischer-Piette, Blanc, Blanc and Salvat, 1994, specimen, Ankarana Reserve. Fig. 32. *G. fischerpiettei s.s.* sp. nov. holotype, Ankarana Reserve. Fig. 33. *G. fischerpiettei enigma* subsp. nov. holotype, Ankarana Reserve. Fig. 34. *G. satisfacta charlesblanci* subsp. nov. holotype, Ankarana Reserve. Fig. 35. *G. satisfacta vitsia* subsp. nov. holotype, Ankarana Reserve. Figs. 36-38. *G. satisfacta satisfacta* Fischer-Piette, Blanc, Blanc and Salvat, 1994, specimens, Ankarana Reserve. Scale bar 1 mm.

lower sutures. Peristome height 5.7 mm, width 4.8 mm (0.7 shell D; peristome H/W 1.2); apertural lip width 0.80 mm (0.16 peristome W). Apertural barriers consisting of a small parietal tooth and a small columellar recessed baffle. Umbilicus imperforate.

Gulella nifikelia sp. nov.
Fig. 2

DIAGNOSIS. *G. nifikelia* sp. nov. is somewhat similar to the South African *G. perspicuaeformis* (Sturany, 1898) but is much more loosely coiled. Of Madagascan *Gulella* with apertural dentition restricted to parietal and palatal teeth, *G. nifikelia* sp. nov. is unique in its combination of (a) parietal and palatal teeth minute and approximately equal in size, (b) shell height less than 4.5 mm (whorls/ln height 4.5), and (c) moderately strong rib sculpturing. Other species have parietal and palatal teeth small to large and generally unequal in size, or if small and approximately equal then

shell height is greater than 6.5 mm (whorls/ln height 3.4) and rib sculpture is very weak to absent.

HOLOTYPE. Station 423 (UF 274964, 1 ad): 23°00'S, 47°44'E: Madagascar: Manombo Reserve, 50 m: rainforest. 21-Apr-95.

DESCRIPTION OF HOLOTYPE. Height 4.0 mm, diameter 1.8 mm (H/D 2.2), whorls 6.2 (whorls/ln height 4.47). Apical angle 75°, barreling 1.1%. Sutural depth 4.4%, sutural crenulation strong. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 2.1, diameter of first 1.5 whorls 0.88 mm, embryonic sculpture smooth, with a trace of growth lines or riblets. Peristome height 1.2 mm, width 1.3 mm (0.7 shell D; peristome H/W 0.9); apertural lip width 0.22 mm (0.17 peristome W). Apertural barriers consisting of a small parietal tooth; a small palatal tooth (parietal-palatal embayment extremely wide); and a small columellar recessed baffle. Umbilicus a very narrow well.

ETYMOLOGY. For the small size of the apertural barriers (Malagasy "nify" = teeth, "kely" = little).

Gulella bouchardi Fischer-Piette, Blanc and Vukadinovic, 1974

Fischer-Piette *et al.* (1994): plate V fig. 1 (holotype)

DIAGNOSIS. Among Madagascan *Gulella* with (a) apertural dentition restricted to parietal and palatal teeth, (b) shell sculpture smooth or nearly so (but with a crenulate suture), and (c) parietal tooth small and parieto-palatal embayment wide, *G. bouchardi* is unique in its very loose coiling (whorls/ln height about 3.1). It is most similar to *G. masoalae*, which has tighter coiling (whorls/ln height 3.3-3.4).

DESCRIPTION OF HOLOTYPE (based on illustration in Fischer-Piette *et al.*, 1994). Height 7.0 mm, diameter 3.1 mm (H/D 2.2), whorls 6.0 (whorls/ln height 3.08). Apical angle 100°, barreling 0.0%. Sutural depth 9.7%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Peristome height 2.2 mm, width 2.0 mm (0.6 shell D; peristome H/W 1.1); apertural lip width 0.30 mm (0.15 peristome W). Apertural barriers consisting of a minute parietal tooth; a small to moderate, triangular palatal tooth (parietal-palatal embayment wide); and a small columellar recessed baffle. Umbilicus a crevice, apparently.

Gulella masoalae sp. nov.

Fig. 3

DIAGNOSIS. *G. masoalae* sp. nov. is somewhat similar to the Comoran *G. diodon* (Morelet, 1882) but is much more loosely coiled. Among Madagascan *Gulella* with (a) apertural dentition restricted to parietal and palatal teeth, (b) shell sculpture smooth or nearly so (but with a crenulate suture), and (c) parietal tooth small and parieto-palatal embayment wide, *G. masoalae* sp. nov. is unique in its coiling (whorls/ln height 3.28-3.35). It is most similar to *G. bouchardi*, which has looser coiling (whorls/ln height 3.1), and to the sometimes sympatric *G. antongilae* sp. nov., which has both tighter coiling (whorls/ln height 3.38-3.58) and a smaller initial whorl (diameter of first 1.5 whorls 1.05-1.13 mm vs. 1.25-1.35 mm in *G. masoalae* sp. nov.). *G. masoalae* sp. nov. is somewhat similar to *G. marojejyae* sp. nov. in size, coiling, and apertural dentition, but is larger in initial-whorl size (diameter of first 1.5 whorls 1.25-1.35 mm *vs.* 1.0-1.1 mm) and has smooth (*vs.* half-ribbed) sculpture.

HOLOTYPE. Station 311 (UF 274928, 1 ad): 15°33'S, 49°59'E: Madagascar: W Masoala Peninsula, 430 m: hardwood rainforest. 27-Sep-95.

DRY PARATYPES. Stations 294 (1 juv, specimen lost); 295 (2 juv, specimens lost); 297 (1 juv, specimen lost); 306 (UF 274929, 1 juv); 307 (ANSP 403446, 1 ad); 308 (1 juv, specimen lost); 309 (15 juv, specimens lost); 310 (1 juv, specimens lost); 311 (UF 274930, 1 juv; AMS C203598, 1 ad]); 313 (MNHN, 1 ad); 314 (UF 274931, 1 ad, 3 juv).

ALCOHOL PARATYPES. Stations 307 (UF 275129, 2 juv); 311 (UF 275130, 2 ad).

DESCRIPTION OF HOLOTYPE. Height 7.8 mm, diameter 3.3 mm (H/D 2.4), whorls 6.9 (whorls/ln height 3.35). Apical angle 80°, barreling 0.0%. Sutural depth 7.5%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.1, diameter of first 1.5 whorls 1.25 mm, embryonic sculpture smooth. Peristome height 2.4 mm, width 2.2 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.23 mm (0.10 peristome W). Apertural barriers consisting of a small parietal tooth; a large, butte-shaped palatal tooth (parietal-palatal embayment wide); and a small columellar recessed baffle. Umbilicus imperforate.

VARIATION. See Table 2.

ETYMOLOGY. For both Masoala National Park and the villagers of Masoala who helped collect.

Gulella antongilae sp. nov.

Figs. 4, 5, 6

DIAGNOSIS. *G. antongilae* sp. nov. is somewhat similar to the Comoran *G. diodon* (Morelet, 1882) but is more loosely coiled and its palatal tooth is lower in position and generally broader and squarer. Among Madagascan *Gulella* with (a) apertural dentition restricted to parietal and palatal teeth, (b) shell sculpture smooth or nearly so (but with a crenulate suture), and (c) parietal tooth small and parieto-palatal embayment wide, *G. antongilae* sp. nov. is unique in its tight coiling (whorls/ln height 3.38-3.58). It is most similar to the sometimes sympatric *G. masoalae* sp. nov., which differs in both its looser coiling (whorls/ln height 3.28-3.35) and its larger initial whorl (diameter of first 1.5

Figs. 39-45. Figs. 39, 40. *Gulella mahia* sp. nov.: Fig. 39 holotype, southern Cap d'Ambre; Fig. 40 paratype, type locality. Fig. 41. *G. ranomasina* sp. nov. holotype, northern Cap d'Ambre. Fig. 42. *G. jaomnai* sp. nov. holotype, southern Cap d'Ambre. Fig. 43. *G. ambrensis s.s.* sp. nov. holotype, Montagne d'Ambre National Park. Fig. 44. *G. ambrensis andavakoerae* subsp. nov. holotype, Andavakoera massif. Fig. 45. *G. ambrensis rakotomalalai* sp. nov. holotype, Analamera Reserve. Scale bar 1 mm.

whorls 1.25-1.35 mm vs. 1.05-1.13 mm in *G. antongilae* sp. nov.).

HOLOTYPE. Station 300 (UF 274776, 1 ad): 15°47'S, 50°03'E: Madagascar: W Masoala Peninsula, 350 m: hardwood rainforest. 20-Sep-95.

FIGURED PARATYPES. Stations 364 (UF 274777, 1 ad); 723 (UF 274782, 1 ad).

OTHER DRY PARATYPES. Stations 294 (UF 274784, 2 ad); 295 (UF 274779, 1 juv); 297 (MNHN, 1 ad, 1 juv); 303 (ANSP 403447, 1 ad); 310 (AMS C203587, 1 ad, 1 juv); 363 (UF 274780, 2 ad; ANSP 403445, 1 ad); 365 (AMS C203605, 1 ad); 366 (UF 274783, 1 ad, 1 juv); 372 (MNHN, 1 juv); 723 (UF 274782, 1 juv); 724 (UF 274778, 1 juv); 756 (UF 274785, 1 ad, 1 juv); 758 (UF 274781, 1 ad).

ALCOHOL PARATYPES. Stations 283 (UF 275074, 1 ad); 285 (UF 275069, 3 ad); 294 (UF 275078, 1 ad, 3 juv); 295 (UF 275072, 1 juv); 300 (UF 275071, 1 juv); 303 (UF 275076, 1 ad, 1 juv); 310 (UF 275073, 2 juv); 363 (UF 275077, 1 ad); 723 (UF 275070, 1 ad); 724 (UF 275075, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 5.9 mm, diameter 2.7 mm (H/D 2.2), whorls 6.2 (whorls/ln height 3.50). Apical angle 85°, barreling 3.5%. Sutural depth 7.0%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 1.10 mm, embryonic sculpture smooth, with faint traces of growth lines. Peristome height 1.6 mm, width 1.7 mm (0.6 shell D; peristome H/W 1.0); apertural lip width 0.19 mm (0.11 peristome W). Apertural barriers consisting of a very small parietal tooth; a moderate, broad, somewhat rectangular palatal tooth (parietal-palatal embayment wide); and a small columellar recessed baffle. Umbilicus imperforate.

VARIATION. See Tables 2, 3, 4.

ETYMOLOGY. For the Baie d'Antongil.

Gulella andreana Fischer-Piette,
Blanc and Vukadinovic, 1974
Fischer-Piette *et al.* (1994): plate V, fig. 2 (holotype)
Fig. 7 (specimen)

DIAGNOSIS. Among Madagascan *Gulella*, there are two species with (a) shell cylindrical and smooth, without sutural crenulation; (b) a columellar recessed baffle that is only shallowly recessed and is nubbed or bifid like a tooth; and (c) other apertural barriers limited to a smallish, sometimes weakly bifid parietal tooth, and a smaller, rounded-nub- or peg-shaped palatal tooth, separated by a wide embayment: *G. andreana* and *G. beandreana* sp. nov. *G. andreana* has a smaller shell for the same number of whorls (whorls/ln height about 3.9 vs. about 3.6) and a smaller initial whorl (diameter of first 1.5 whorls 0.9 mm vs. 1.1) than *G. beandreana* sp. nov.

FIGURED SPECIMEN. Station 32 (UF 274763, 1 ad).

OTHER DRY VOUCHER SPECIMENS. Stations 32 (UF 274723, 4 ad, 4 juv); 42 (UF 274700, 1 ad); 43 (UF 274740, 2 ad, 6 juv); 49 (UF 274693, 1 ad); 55 (UF 274720, 7 ad, 5 juv); 56 (UF 274710, 4 ad, 2 juv); 58 (UF 274762, 4 ad, 3 juv); 61 (UF 274715, 73 ad, 91 juv; AMS C203566, 5 ad; ANSP 403448, 5 ad; MNHN, 5 ad); 62 (UF 274717, 94 ad, 50 juv); 63 (UF 274719, 91 ad, 87 juv); 64 (UF 274738, 1 ad, 1 juv); 65 (UF 274701, 10 ad, 1 juv); 68 (UF 274734, 18 ad, 17 juv); 69 (UF 274711, 6 ad, 2 juv); 70 (UF 274702, 5 ad, 3 juv); 71 (UF 274750, 4 ad); 72 (UF 274744, 1 ad, 3 juv); 81 (UF 274698, 1 juv); 82 (UF 274736, 4 ad, 7 juv); 83 (UF 274716, 52 ad, 88 juv); 84 (UF 274718, 24 ad, 29 juv); 168 (UF 274721, 3 ad); 218 (UF 274735, 5 ad, 9 juv); 221 (UF 274755, 8 ad); 222 (UF 274737, 3 ad, 2 juv); 233 (UF 274764, 2 ad, 1 juv); 234 (UF 274741, 3 ad, 1 juv); 238 (UF 274766, 10 ad, 2 juv); 239 (UF 274752, 1 ad); 241 (UF 274747, 1 ad); 252 (UF 274745, 3 ad, 1 juv); 254 (UF 274728, 5 ad, 17 juv); 255 (UF 274732, 4 ad, 8 juv); 400 (UF 274757, 3 ad, 2 juv); 401 (UF 274714, 1 ad, 1 juv); 403 (UF 274746, 1 ad, 1 juv); 404 (UF 274713, 1 ad, 2 juv); 408 (UF 274726, 15 ad, 2 juv); 411 (UF 274759, 3 ad, 2 juv); 439 (UF 274749, 11 ad, 4 juv); 440 (UF 274754, 6 ad, 1 juv); 441 (UF 274739, 2 ad, 4 juv); 442 (UF 274709, 12 ad, 5 juv); 443 (UF 274722, 8 ad, 3 juv); 444 (UF 274705, 4 ad, 1 juv); 445 (UF 274724, 8 ad, 1 juv); 447 (UF 274765, 1 ad, 1 juv); 448 (UF 274697, 3 ad, 2 juv); 449 (UF 274758, 3 ad); 450 (UF 274748, 5 ad); 451 (UF 274761, 6 ad, 3 juv); 458 (UF 274695, 3 ad); 459 (UF 274712, 10 ad); 460 (UF 274696, 3 ad, 2 juv); 461 (UF 274751, 10 ad, 4 juv); 462 (UF 274760, 2 ad, 2 juv); 463 (UF 274707, 1 ad, 1 juv); 466 (UF 274725, 1 ad, 2 juv); 483 (UF 274753, 2 ad, 2 juv); 484 (UF 274694, 1 juv); 489 (UF 274699, 3 ad, 4 juv); 494 (UF 274704, 7 ad, 19 juv); 558 (UF 274730, 4 ad, 4 juv); 565 (UF 274703, 2 ad, 1 juv); 570 (UF 274756, 7 ad, 14 juv); 572 (UF 274742, 1 ad); 803 (UF 274727, 1 ad, 2 juv); 810 (UF 274708, 1 ad); 813 (UF 274731, 7 ad, 10 juv); 815 (UF 274706, 4 ad); 816 (UF 274729, 3 juv); 818 (UF 274733, 5 ad, 5 juv).

ALCOHOL VOUCHER SPECIMENS. Stations 52 (UF 273694, 1 ad); 61 (UF 273710, 2 ad, 2 juv); 62 (UF 273696, 4 ad); 63 (UF 273704, 2 ad); 400 (UF 273709, 1 ad); 408 (UF 273711, 5 ad); 443 (UF 273697, 11 ad, 1 juv); 444 (UF 273701, 5 ad, 1 juv); 445 (UF 273703, 1 ad, 2 juv); 446 (UF 273702, 2 ad, 2 juv); 447 (UF 273708, 14 ad, 2 juv); 448 (UF 273700, 22 ad); 449 (UF 273695, 11 ad, 8 juv); 450 (UF 273690, 18 ad, 3 juv); 451 (UF 273698, 6 ad, 3 juv); 458 (UF 273692, 2 ad); 459 (UF 273693, 5 ad); 460 (UF 273713, 6 ad, 1 juv); 461 (UF 273705, 8 ad, 4 juv); 462 (UF 273706, 15 ad, 7 juv); 463 (UF 273714, 12 ad, 2 juv); 464 (UF 273707, 9 ad, 11 juv); 465 (UF uncatalogued, 5 ad, 3 juv, possibly lost); 466 (UF 273712, 7 ad, 6 juv); 565 (UF 273699, 1 juv).

DESCRIPTION OF HOLOTYPE (based on illustration in Fischer-Piette *et al.*, 1994). Height 6.5 mm, diameter 1.9 mm (H/D 3.5), whorls 7.0 (whorls/ln height 3.74). Apical angle 90°, barreling -8.3%. Sutural depth 5.4%, sutural crenulation none. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Peristome height 1.7 mm, width 1.6 mm (0.8 shell D; peristome H/W 1.1); apertural lip width 0.20 mm (0.08 peristome W). Apertural barriers consisting of a moderate parietal tooth; a small, peg-triangular palatal tooth (parietal-palatal embayment wide); and a small, nubbed, shallowly recessed columellar recessed baffle.

Gulella beandreana sp. nov.
Figs. 8, 9

DIAGNOSIS. Among Madagascan *Gulella*, there are two species with (a) shell cylindrical and smooth, without sutural crenulation; (b) a columellar recessed baffle that is only shallowly recessed and is nubbed or bifid like a tooth; and (c) other apertural dentition limited to a smallish, sometimes weakly bifid parietal tooth, and a smaller, rounded-nub- or peg-shaped palatal tooth, separated by a wide

Figs. 46-52. Fig. 46. *Gulella ambrensis capdambri* subsp. nov. holotype, northern Cap d'Ambre. Fig. 47. *G. ambrensis orangea* subsp. nov. holotype, Forêt d'Orange, Cap Mine. Fig. 48. *G. capmini* sp. nov. paratype, Cap Mine. Fig. 49. *G. bemarahae* sp. nov. holotype, Bemaraha Reserve. Fig. 50. *G. nakamaroa* sp. nov. holotype, Ankarana Reserve. Fig. 51. *G. capmini* sp. nov. holotype, Cap Mine. Fig. 52. *G. marojejyae* sp. nov. holotype, Marojejy Reserve. All scale bars 1 mm.

embayment: *G. beandreana* sp. nov. and *G. andreana*. *G. beandreana* sp. nov. is a rainforest species, and has a larger shell for the same number of whorls (whorls/ln height about 3.6 vs. about 3.9) and a larger initial whorl (diameter of first 1.5 whorls 1.1 mm vs. 0.9) than *G. andreana*, which is primarily a deciduous-forest species.

HOLOTYPE. Station 434 (UF 274786, 1 ad): 23°00'S, 47°44'E: Madagascar: Manombo Reserve, 50 m: rainforest. 23-Mar-96.

FIGURED PARATYPE. Station 712 (UF 274788, 1 ad).

OTHER DRY PARATYPES. Stations 677 (UF 274792, 2 ad, 1 juv); 679 (UF 274794, 8 ad, 2 juv); 680 (UF 274793, 10 ad; AMS C203568, 1 ad; ANSP 403449, 1 ad; MNHN, 1 ad); 712 (UF 274789, 3 ad, 1 juv); 715 (UF 274795, 3 ad, 1 juv); 716 (UF 274790, 1 ad); 717 (UF 274791, 4 ad, 2 juv).; 1402 (UF 274787, 1 ad).

ALCOHOL PARATYPES. Stations 435 (UF 275080, 2 ad); 679 (UF 275079, 1 ad); 717 (UF 275081, 1 juv).

DESCRIPTION OF HOLOTYPE. Height 6.9 mm, diameter 2.4 mm (H/D 2.9), whorls 6.9 (whorls/ln height 3.56). Apical angle 105°, barreling -1.3%. Sutural depth 2.7%, sutural crenulation none. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.1, diameter of first 1.5 whorls 1.11 mm, embryonic sculpture smooth. Peristome height 2.0 mm, width 2.0 mm (0.8 shell D; peristome H/W 1.0); apertural lip width 0.22 mm (0.11 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, nub-shaped palatal tooth (parietal-palatal embayment wide); and a small, nubbed, bifid, shallowly recessed columellar recessed baffle. Umbilicus imperforate.

VARIATION. Columellar recessed baffle sometimes undivided.

ETYMOLOGY. For its resemblance to a large (Malagasy "be") version of *Gulella andreana*.

Gulella constricta sp. nov.
Fig. 10

DIAGNOSIS. Unique in having its aperture constricted centrally into an hourglass shape, and, amongst Madagascan *Gulella* with apertural dentition restricted to a parietal and a palatal tooth, in having its parietal tooth deeply recessed.

HOLOTYPE. Station 527 (UF 274820, 1 ad): 13°59'S, 48°47'E: Madagascar: Tsaratanana Reserve, 1395 m: rainforest. 17-Jun-95.

DESCRIPTION OF HOLOTYPE. Height 4.4 mm, diameter 1.8 mm (H/D 2.5), whorls 6.4 (whorls/ln height 4.35). Apical angle 115°, barreling 2.3%. Sutural depth 9.1%, sutural crenulation moderate. In apertural view, penultimate and body whorls with strong rib sculpture that diminishes completely between upper and lower sutures. Embryonic whorls 2.1, diameter of first 1.5 whorls 0.74 mm, embryonic sculpture of sutural notches. Aperture and peristome with a unique hourglass shape. Peristome height 1.3 mm, width 1.0 mm (0.6 shell D; peristome H/W 1.2); apertural lip width 0.12 mm (0.12 peristome W). Apertural barriers consisting of a massive, deeply recessed parietal tooth; a moderate, low and wide palatal tooth (parietal-palatal embayment narrow); and a small columellar recessed baffle. Umbilicus a crevice.

ETYMOLOGY. For the constricted (Latin "constricta") aperture.

Gulella ambatovakiae sp. nov.
Fig. 12

DIAGNOSIS. Among Madagascan *Gulella* with (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent or weak, and (c) rib sculpture weak to none, *G. ambatovakiae* sp. nov. is unique in both its bifid parietal tooth and its triangular aperture.

HOLOTYPE. Station 766 (UF 274658, 1 ad): 16°43'S, 49°23'E: Madagascar: Ambatovaky Reserve, 400 m: rainforest. 27-Nov-95.

DESCRIPTION OF HOLOTYPE (broken and missing apex). Height (estimated) 4.6 mm, diameter (estimated) 2.3 mm (H/D 2.0). Barreling 2.7%. Sutural depth 10.5%, sutural crenulation apparently weak (but nearly completely eroded away). In apertural view, penultimate and body whorls smoothish, without rib sculpture. Peristome height 1.2 mm, width 1.4 mm (0.6 shell D; peristome H/W 0.8); apertural lip width 0.18 mm (0.12 peristome W). Apertural barriers consisting of a moderate, bifid parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); and a small columellar recessed baffle. Umbilicus imperforate.

ETYMOLOGY. For Ambatovaky Reserve.

Gulella magnifica sp. nov.
Fig. 11

DIAGNOSIS. *G. magnifica* sp. nov. is similar in shape and aperture to the Comoran *G. modioliformis* (Morelet, 1877) but has very much tighter coiling. Among Madagascan *Gulella* with (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella nonexistent or weak, and (c) rib sculpture weak to none, *G. magnifica* sp. nov. is unique in its great shell size (height greater than 11 mm) and large initial whorl (diameter of first 1.5 whorls 1.5 mm).

HOLOTYPE. Station 803 (UF 274879, 1 ad): 13°00'S, 49°01'E: Madagascar: Ankarana Reserve, 50 m. 8-Oct-94.

DRY PARATYPES. Stations 802 (AMS C203589, 1 ad; MNHN, 1 ad); 803 (UF 274880, 7 juv; AMS C203590, 8 juv); 807 (AMS C203591, 1 ad, 1 juv; ANSP 403450, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 12.6 mm, diameter 4.5 mm (H/D 2.8), whorls 9.3 (whorls/ln height 3.67). Apical angle 90°, barreling 4.4%. Sutural depth

Figs. 53-58. Fig. 53. *Gulella griffithsi* sp. nov. holotype, Bemaraha Reserve. Fig. 54. *G. tsara* sp. nov. holotype, Tsaratanana Reserve. Fig. 55. *G. microstriata* sp. nov. holotype, Ankarana Reserve. Fig. 56. *G. kelibea* sp. nov. holotype, Manombo Reserve. Fig. 57. *G. analamerae* sp. nov. holotype, Analamera Reserve. Fig. 58. *G. vohimarae* sp. nov. holotype, south of Vohimar. All scale bars 1 mm.

2.1%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.7, diameter of first 1.5 whorls 1.50 mm, embryonic sculpture of minute riblets, stronger above the suture, but faint throughout. Peristome height 3.3 mm, width 3.2 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.60 mm (0.19 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); and a small columellar recessed baffle. Umbilicus an extremely minute crevice.

ETYMOLOGY. For the grand and splendid (Latin "magnifica") shell.

Gulella pseudandreana sp. nov.
Fig. 13

DIAGNOSIS. Among Madagascan *Gulella*, there are two species with (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent or weak, and (c) general rib sculpture weak but conspicuous: *G. pseudandreana* sp. nov. and *G. gallorum*. *G. pseudandreana* sp. nov. differs from *G. gallorum* in its smaller initial whorl (diameter of first 1.5 whorls 1.000-1.112 mm vs. 1.225-1.325 mm). *G. pseudandreana* differs from the similar *G. jaominai* sp. nov. in its weakly ribbed sculpture (*vs.* smooth sculpture) and its larger initial whorl (diameter of first 1.5 whorls 1.000-1.112 mm *vs.* 0.912-0.938 mm). In its size, coiling tightness, and columnar shape, *G. pseudandreana* sp. nov. bears superficial resemblance to *G. andreana*, from which it differs in its well recessed, broadly rounded columellar recessed baffle (*vs.* shallow, nubbed, and tooth-like), its sculpture of weak ribs (*vs.* smooth), and its larger initial whorl (diameter of first 1.5 whorls 1.0-1.1 *vs.* about 0.9).

HOLOTYPE. Station 245 (UF 274975, 1 ad): 19°08'S, 44°48'E: Madagascar: S Bemaraha Reserve, 70 m: dry forest. 14-Jun-95.

DRY PARATYPES. Stations 247 (UF 274978, 14 ad, 15 juv); 249 (UF274976, 4 ad, 7 juv; AMS C203607, 7 ad, 6 juv; ANSP 403451, 1 ad; MNHN, 1 ad); 250 (UF 274977, 3 ad, 5 juv); 251 (UF 274979, 1 ad, 3 juv).

DESCRIPTION OF HOLOTYPE. Height 6.3 mm, diameter 2.3 mm (H/D 2.8), whorls 7.2 (whorls/ln height 3.87). Apical angle 85°, barreling -1.4%. Sutural depth 4.2%, sutural crenulation moderate. In apertural view, penultimate and body whorls with weak rib sculpture that diminishes about three-fourths between upper and lower sutures. Embryonic whorls 2.2, diameter of first 1.5 whorls 1.11 mm, embryonic sculpture of faint growth lines or riblets. Peristome height 1.8 mm, width 1.8 mm (0.8 shell D; peristome H/W 1.0); apertural lip width 0.25 mm (0.14 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, rounded-triangular palatal tooth (parietal-palatal embayment fairly wide); and a small columellar recessed baffle. Umbilicus a crevice.

VARIATION.

Station	#Sn	Wh/lnHt	D1st1.5Wh
245	1	3.87	1.11
247	2	3.78-3.94	1.00-1.05
249	2	3.67-3.74	1.05-1.10

ETYMOLOGY. For its false (Greek "pseud-") resemblance to *Gulella andreana*.

Gulella gallorum Fischer-Piette, Blanc and Salvat, 1975
Fischer-Piette *et al.* (1994): plate IV, figs. 15-18 (holotype)
Fig. 14 (specimen)

DIAGNOSIS. Among Madagascan *Gulella*, there are two species with (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent or weak, and (c) general rib sculpture weak but conspicuous: *G. gallorum* and *G. pseudandreana* sp. nov., which also are similar in their cylindrical-to-columnar shapes. *G. gallorum* differs from *G. pseudandreana* sp. nov. in its larger initial whorl (diameter of first 1.5 whorls 1.225-1.325 mm *vs.* 1.000-1.112 mm). *G. gallorum* differs from the similar and sometimes sympatric *G. jaominai* sp. nov. in its weakly ribbed sculpture (*vs.* smooth sculpture), its looser coiling (whorls/ln height 3.71-3.90 *vs.* 3.90-3.98), and, especially, its much larger initial whorl (diameter of first 1.5 whorls 1.225-1.325 mm vs. 0.912-0.938 mm). *G. gallorum* differs from the similar *G. boucheti* (both of which occur on Montagne des Français: Fischer-Piette *et al.*, 1994) in its distinctly cylindrical (*vs.* barreled) shape and seemingly in its smaller initial whorl (diameter of first 1.5 whorls 1.22-1.32 mm *vs.* 1.35-1.36 mm).

FIGURED SPECIMEN. Station 401 (UF 274831, 1 ad).

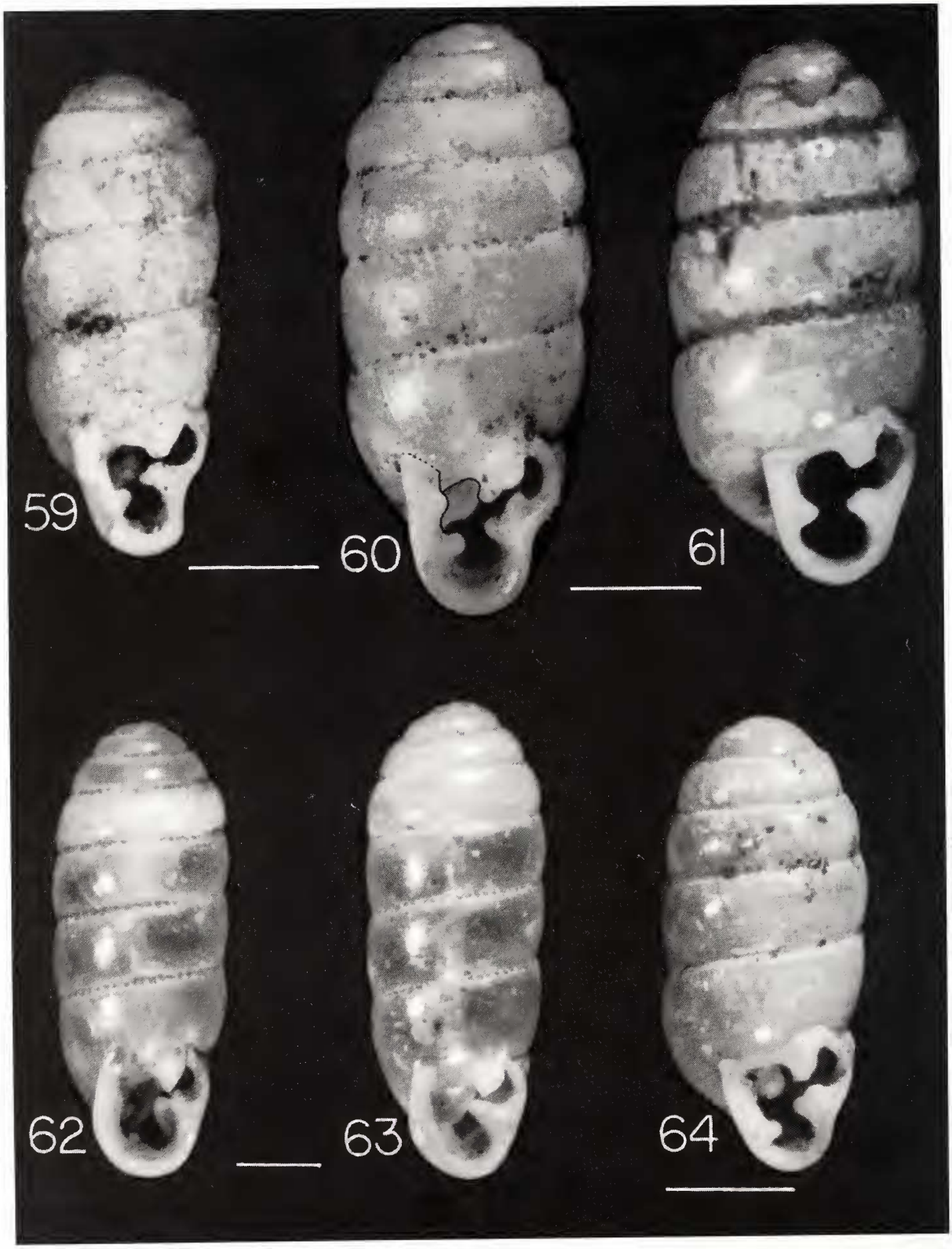
OTHER DRY VOUCHER SPECIMENS. Stations 401 (UF 274832, 68 ad, 46 juv; AMS C203584, 3 ad; ANSP 403452, 3 ad; MNHN, 3 ad); 405 (UF 274833, 4 ad, 5 juv).

DESCRIPTION OF HOLOTYPE (from illustration in Fischer-Piette *et al.*, 1994). Height 9.2 mm, diameter 2.8 mm (H/D 3.2), whorls 8.3 (whorls/ln height 3.74). Apical angle 75°, barreling 0.0%. Sutural depth 8.0%, sutural crenulation moderate. In apertural view, penultimate and body whorls with weak rib sculpture that does not diminish between upper and lower sutures. Peristome height 2.3 mm, width 2.2 mm (0.8 shell D; peristome H/W 1.0); apertural lip width 0.20 mm (0.07 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate to large, squared palatal tooth (parietal-palatal embayment moderately wide); and a small columellar recessed baffle.

VARIATION. See Table 2.

Gulella rakotoarisoni sp. nov.
Fig. 15

DIAGNOSIS. Among Madagascan *Gulella* species with (a) apertural dentition restricted to a parietal tooth and a



Figs. 59-64. Fig. 59. *Gulella teudronia* sp. nov. holotype, Analamera Reserve. Fig. 60. *G. celestinae* sp. nov. holotype, Namoroka Reserve. Fig. 61. *G. nosybei* sp. nov. holotype, Lokobe Reserve, Nosy Be. Fig. 62. *G. bemoka* sp. nov. holotype, northern Cap d'Ambre. Fig. 63. *G. vavakelia* sp. nov. holotype, Analamera Reserve. Fig. 64. *G. uitsikia* sp. nov. holotype, Ankarana Reserve. All scale bars 1 mm.

palatal tooth, (b) baso-columellar lamella non-existent or weak, (c) rib sculpture absent or weak and inconspicuous, (d) height less than 9 mm and diameter of first 1.5 whorls less than 1.4 mm, and (e) shell with height/diameter 2.6 or less and barreled to slightly columnar, *G. rakotoarisoni* sp. nov. is unique for its very large parietal and palatal teeth and its conspicuous columellar recessed baffle. *G. rakotoarisoni* sp. nov. bears some resemblance to *G. zanaharyi* sp. nov., but differs in its much smaller columellar recessed baffle and its lack of either a strong baso-columellar lamella or a baso-columellar tooth.

HOLOTYPE. Station 580 (UF 274980, 1 ad): 12°58'S, 49°05'E: Madagascar: Ankarana Reserve, 95 m: dry deciduous forest. 26-Aug-95.

DRY PARATYPES. Stations 570 (UF 274981, 1 ad, 1 juv); 572 (ANSP 403453, 1 ad, 1 juv); 580 (AMS C203608, 1 ad, 1 juv); 581 (MNHN, 1 ad, 3 juv).

DESCRIPTION OF HOLOTYPE. Height 4.4 mm, diameter 1.9 mm (H/D 2.4), whorls 6.1 (whorls/ln height 4.09). Apical angle 95°, barreling 1.1%. Sutural depth 4.3%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.93 mm, embryonic sculpture smooth. Peristome height 1.4 mm, width 1.4 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.29 mm (0.21 peristome W). Apertural barriers consisting of a large parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment moderately wide); and a small columellar recessed baffle. Umbilicus imperforate, apparently.

ETYMOLOGY. For Jean Rakotoarison, Projet Parc National de Ranomafana, trusty and hard-working associate in both field and lab, who helped collect this species.

Gulella boucheti Fischer-Piette, Blanc, Blanc and Salvat, 1994
Fischer-Piette *et al.* (1994): fig. 55 (holotype)
Figs. 16, 17 (specimens)

DIAGNOSIS. Two species of Madagascan *Gulella* share (a) apertural dentition restricted to a moderate-sized parietal tooth and a moderate-sized palatal tooth, (b) baso-columellar lamella absent or weak, (c) general rib sculpture absent to weak and inconspicuous, (d) height less than 9 mm, (e) shell with height/diameter 2.6 or less and barreled to slightly columnar, (f) columellar recessed baffle inconspicuous or not visible in apertural view, (g) palatal tooth low, broad, and squarish, (h) sutures shallowly impressed, (i) embryonic whorls 1.6 to 1.7, and (j) diameter of first 1.5 whorls 1.2 to 1.4 mm: *G. boucheti* and *G. petitboucheti* sp. nov. *G. boucheti* is distinctly more loosely coiled than *G. petitboucheti* sp. nov. (whorls/ln height about 3.6-3.8 *vs.* about 4.3) and has a larger initial whorl (diameter of first 1.5 whorls about 1.4 mm *vs.* about 1.2 mm). *G. boucheti* differs from the similar *G. gallorum* (both of which occur on Montagne des Français: Fischer-Piette *et al.*, 1994) in its barreled (*vs.* cylindrical) shape and seemingly in its larger initial whorl (diameter of first 1.5 whorls 1.35-1.36 mm *vs.* 1.22-1.32 mm). *G. boucheti* resembles *G. lohabea* sp. nov. but lacks its baso-columellar lamella and has a larger initial whorl (diameter of first 1.5 whorls 1.35-1.36 mm *vs.* 1.28 mm).

FIGURED SPECIMENS. Stations 218 (UF 274810, 1 ad); 222 (UF 274809, 1 ad).

OTHER DRY VOUCHER SPECIMENS. Stations 217 (UF 274813, 9 ad, 2 juv); 218 (UF 274814, 6 ad, 4 juv); 221 (UF 274812, 320 ad, 30 juv; AMS C203573, 5 ad; ANSP 403454, 5 ad; MNHN, 5 ad); 222 (UF 274811, 8 ad).

ALCOHOL VOUCHER SPECIMENS. Stations 221 (UF 275083, 29 ad, 6 juv); 222 (UF 275082, 1 juv).

DESCRIPTION OF HOLOTYPE (based on illustration in Fischer-Piette *et al.*, 1994, which seems to be a neoadult with aperture not fully developed). Height 6.4 mm, diameter 2.9 mm (H/D 2.2), whorls 7.0 (whorls/ln height 3.77). Apical angle 85°, barreling 12.9%. Sutural depth 3.2%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Peristome height 1.6 mm, width 1.8 mm (0.6 shell D; peristome H/W 0.9); apertural lip width 0.20 mm (0.08 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate to large, triangular palatal tooth (parietal-palatal embayment fairly wide); and a small columellar recessed baffle. Umbilicus a crevice.

VARIATION. See Tables 2, 3.

Gulella petitboucheti sp. nov.
Fig. 18

DIAGNOSIS. There are only two species of Madagascan *Gulella* with (a) apertural dentition restricted to a moderate-sized parietal tooth and a moderate-sized palatal tooth, (b) baso-columellar lamella non-existent or weak, (c) general rib sculpture absent or weak and inconspicuous, (d) height less than 9 mm, (e) shell with height/diameter 2.6 or less and barreled to slightly columnar, (f) columellar recessed baffle inconspicuous or not visible, (g) palatal tooth low, broad, and squarish, (h) sutures shallowly impressed, (i) embryonic whorls 1.6 to 1.7, and (j) diameter of first 1.5 whorls 1.2 to 1.4 mm: *G. petitboucheti* sp. nov. and *G. boucheti*. *G. petitboucheti* sp. nov. is distinctly more tightly coiled than *G. boucheti* (whorls/ln height about 4.3 *vs.* about 3.6-3.8) and has a smaller initial whorl (diameter of first 1.5 whorls about 1.2 mm *vs.* about 1.4 mm).

HOLOTYPE. Station 223 (UF 274972, 1 ad): 12°18'S, 49°20'E: Madagascar: Montagne des Français, 70 m: dry deciduous forest. 21-Jul-95.

DRY PARATYPES. Stations 222 (UF 274973, 4 ad); 223 (UF 274974, 1 ad, 3 juv; AMS C203606, 1 ad; ANSP 403455, 1 ad; MNHN, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 5.5 mm, diam-

Figs. 65-70. Figs. 65-67. *Gulella bobaombiae* sp. nov.: Fig. 65 holotype, southern Cap d'Ambre; Fig. 66 paratype, Montagne des Français; Fig. 67 paratype, northern tip of Cap d'Ambre. Fig. 68. *G. ambanikelia* sp. nov. holotype, Ankarana Reserve. Figs. 69-70. *G. zanaharyi* sp. nov. paratypes: Fig. 69 northern Cap d'Ambre; Fig. 70 southern Cap d'Ambre. All scale bars 1 mm.

eter 2.4 mm (H/D 2.3), whorls 7.4 (whorls/ln height 4.34). Apical angle 95°, barreling 7.7%. Sutural depth 3.8%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.6, diameter of first 1.5 whorls 1.18 mm, embryonic sculpture smooth. Peristome height 1.7 mm, width 1.6 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.21 mm (0.13 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, very low, rounded-rectangular palatal tooth (parietal-palatal embayment fairly wide); and a small columellar recessed baffle. Umbilicus a crevice.

VARIATION. See Table 2.

ETYMOLOGY. For its resemblance to a miniature *Gulella boucheti*, with which this species is sympatric.

Gulella reeae Emberton and Pearce, 2000
Fig. 19

DIAGNOSIS. Among Madagascan *Gulella* with (a) apertural dentition restricted to a moderate-sized parietal tooth and a moderate-sized palatal tooth, (b) baso-columellar lamella absent to weak, (c) general rib sculpture absent to weak and inconspicuous, (d) height less than 9 mm, (e) shell with height/diameter 2.6 or less and barreled to slightly columnar, (f) columellar recessed baffle inconspicuous or not visible, (g) palatal tooth elevated, narrow, and triangular or pegged, (h) sutures moderately impressed, (i) embryonic whorls 1.8 to 2.2, and (j) diameter of first 1.5 whorls 0.8 to 1.0 mm, three species are distinguished from *G. fotobohitrae* sp. nov. and *G. razafyi* sp. nov. by their tighter coiling (whorls/ln height 4.4-4.7 *vs.* 4.0-4.3): *G. reeae, G. miaranoniae* sp. nov., and *G. bebokae* sp. nov. *G. reeae* differs from the latter two in its larger initial whorl (diameter of first 1.5 whorls about 0.95 mm *vs.* about 0.80-0.81 mm) and its weak (*vs.* strong) sutural crenulation.

DESCRIPTION OF HOLOTYPE (USNM 860807). Height 4.4 mm, diameter 1.8 mm (H/D 2.4), whorls 6.5 (whorls/ln height 4.36). Apical angle 75°, barreling 0.0%. Sutural depth 7.4%, sutural crenulation weak. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.94 mm, embryonic sculpture smooth, with a faint trace of growth lines or riblets. Peristome height 1.3 mm, width 1.3 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.27 mm (0.20 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, triangular palatal tooth (parietal-palatal embayment wide); and a small columellar recessed baffle. Umbilicus a crevice.

Gulella miaranoniae sp. nov.
Fig. 20

DIAGNOSIS. Among Madagascan *Gulella* with (a) apertural dentition restricted to a moderate-sized parietal tooth and a moderate-sized palatal tooth, (b) baso-columellar lamella absent to weak, (c) general rib sculpture absent to weak and inconspicuous, (d) height less than 9 mm, (e) shell with height/diameter 2.6 or less and barreled to slightly columnar, (f) columellar recessed baffle inconspicuous or not visible, (g) palatal tooth elevated, narrow, and triangular or pegged, (h) sutures moderately impressed, (i) embryonic whorls 1.8 to 2.2, and (j) diameter of first 1.5 whorls 0.8 to 1.0 mm, three species are distinguished from both *G. fotobohitrae* sp. nov. and *G. razafyi* sp. nov. by their tighter coiling (whorls/ln height 4.4-4.7 *vs.* 4.0-4.3): *G. miaranoniae* sp. nov., *G. reeae*, and *G. bebokae* sp. nov. *G. miaranoniae* differs from *G. reeae* in its smaller initial whorl (diameter of first 1.5 whorls about 0.80-0.81 mm *vs.* about 0.95 mm) and its strong (*vs.* weak) sutural crenulation. *G. miaranoniae* differs from *G. bebokae* in its looser coiling (whorls/ln height about 4.5 *vs.* about 4.7), proportionally smaller peristome (0.5 *vs.* 0.7 shell diameter), and rainforest (*vs.* semi-deciduous forest) habitat.

HOLOTYPE. Station 446 (UF 274932, 1 ad): 21°10'S, 47°33'E: Madagascar: Miaranony, E Ranomafana National Park, 630 m: rainforest. 28-Nov-95.

DRY PARATYPES. Stations 439 (UF 274933, 2 ad); 440 (AMS C203610, 1 ad); 441 (UF 274935, 1 ad, 2 juv); 443 (MNHN, 1 ad); 446 (ANSP 403456, 1 ad); 447 (UF 274936, 1 ad); 451 (UF 274935, 2 juv).

ALCOHOL PARATYPE. Station 443 (UF 275131, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 3.9 mm, diameter 1.8 mm (H/D 2.2), whorls 6.2 (whorls/ln height 4.52). Apical angle 95°, barreling 0.0%. Sutural depth 5.8%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.1, diameter of first 1.5 whorls 0.81 mm, embryonic sculpture smooth. Peristome height 0.9 mm, width 0.8 mm (0.5 shell D; peristome H/W 1.0); apertural lip width 0.22 mm (0.27 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, rounded-peg-shaped palatal tooth (parietal-palatal embayment moderately wide); and a small columellar recessed baffle. Umbilicus minute.

VARIATION.

Station	#Sn	Wh/lnHt	D1st1.5Wh
439	1	4.54	0.80
446	1	4.52	0.81
447	1	4.48	0.81

ETYMOLOGY. For the forest and village of Miaranony, on the border of Ranomafana National Park.

Gulella bebokae sp. nov.
Fig. 21

DIAGNOSIS. Among Madagascan *Gulella* with (a) apertural dentition restricted to a moderate-sized parietal tooth and a moderate-sized palatal tooth, (b) baso-columellar lamella absent to weak, (c) general rib sculpture absent to weak and inconspicuous, (d) height less than 9 mm, (e)

Figs. 71-78. Figs. 71-74. *Gulella ambalaniranae* sp. nov. (to same size scale): Fig. 71 holotype, Mount Ambalanirana; Figs. 72-74 paratypes, near Mount Ambalanirana. Fig. 75. *G. namorokae* sp. nov. holotype, Namoroka Reserve. Figs. 76-78. *G. mihomehia* sp. nov. (to same size scale): Fig. 76 holotype, Ankarana Reserve; Fig. 77, 78 paratypes, Ankarana Reserve. All scale bars 1 mm.

shell with height/diameter 2.6 or less and barreled to slightly columnar, (f) columellar recessed baffle inconspicuous or not visible, (g) palatal tooth elevated, narrow, and triangular or pegged, (h) sutures moderately impressed, (i) embryonic whorls 1.8 to 2.2, and (j) diameter of first 1.5 whorls 0.8 to 1.0 mm, three species are distinguished from both *G. fotobohitrae* sp. nov. and *G. razafyi* sp. nov. by their tighter coiling (whorls/ln height 4.4-4.7 *vs.* 4.0-4.3): *G. bebokae* sp. nov., *G. reeae*, and *G. miaranoniae* sp. nov. *G. bebokae* sp. nov. differs from *G. reeae* in its smaller initial whorl (diameter of first 1.5 whorls about 0.80 mm *vs.* about 0.95 mm) and its strong (*vs.* weak) sutural crenulation. *G. bebokae* sp. nov. differs from *G. miaranoniae* sp. nov. in its tighter coiling (whorls/ln height about 4.7 *vs.* about 4.5), proportionally larger peristome (0.7 vs. 0.5 shell diameter), and semi-deciduous forest (*vs.* rainforest) habitat.

HOLOTYPE. Station 494 (UF 274796, 1 ad): 18°45'S, 44°45'E: Madagascar: N Bemaraha Reserve, 280 m: semi-deciduous forest. 29-Jun-96.

DRY PARATYPES. Station 494 (UF 274797, 1 ad, 1 juv; AMS C203569, 1 ad; MNHN, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 3.7 mm, diameter 1.7 mm (H/D 2.2), whorls 6.1 (whorls/ln height 4.67). Apical angle 115°, barreling 4.5%. Sutural depth 6.8%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.80 mm, embryonic sculpture smooth. Peristome height 1.2 mm, width 1.3 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.16 mm (0.13 peristome W). Apertural barriers consisting of a moderate parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment moderately wide); and a small columellar recessed baffle. Umbilicus a crevice.

ETYMOLOGY. For the Beboka River, Bemaraha Reserve.

Gulella fotobohitrae sp. nov.
Fig. 22

DIAGNOSIS. Among Madagascan *Gulella* with (a) apertural dentition restricted to a moderate-sized parietal tooth and a moderate-sized palatal tooth, (b) baso-columellar lamella absent to weak, (c) general rib sculpture absent to weak and inconspicuous, (d) height less than 9 mm, (e) shell with height/diameter 2.6 or less and barreled to slightly columnar, (f) columellar recessed baffle inconspicuous or not visible, (g) palatal tooth elevated, narrow, and triangular or pegged, (h) sutures moderately impressed, (i) embryonic whorls 1.8 to 2.2, and (j) diameter of first 1.5 whorls 0.8 to 1.0 mm, two species are distinguished from *G. reeae, G. miaranoniae* sp. nov., and *G. bebokae* sp. nov. by their looser coiling (whorls/ln height 4.0-4.3 *vs.* 4.4-4.7): *G. fotobohitrae* sp. nov. and *G. razafyi* sp. nov. *G. fotobohitrae* sp. nov. differs from *G. razafyi* sp. nov. in its looser coiling (whorls/ln height 4.0 *vs.* 4.2-4.3) and larger initial whorl (diameter of first 1.5 whorls 0.92-1.01 mm *vs.* 0.84 mm).

HOLOTYPE. Station 1389 (UF 274829, 1 ad): 21°21'S, 47°51'E: Madagascar: Fotobohitra, 350 m. 27-Sep-92.

DRY PARATYPES. Stations 1389 (AMS C203579, 1 ad; ANSP 403457, 1 ad); 1391 (ANSP 403458, 1 ad).

DESCRIPTION OF HOLOTYPE (an eroded shell). Height 5.8 mm, diameter 2.7 mm (H/D 2.2), whorls 7.0 (whorls/ln height 3.99). Apical angle 105°, barreling 3.5%. Sutural depth 4.9%, sutural crenulation moderate. In apertural view, penultimate and body whorls with strong rib sculpture that diminishes completely between upper and lower sutures. Embryonic whorls 2.1, diameter of first 1.5 whorls 1.01 mm, embryonic sculpture smooth. Peristome height 2.0 mm, width 1.7 mm (0.6 shell D; peristome H/W 1.2); apertural lip width 0.34 mm (0.21 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, triangular palatal tooth (parietal-palatal embayment moderately wide); and a small columellar recessed baffle. Umbilicus a very narrow crevice.

VARIATION.

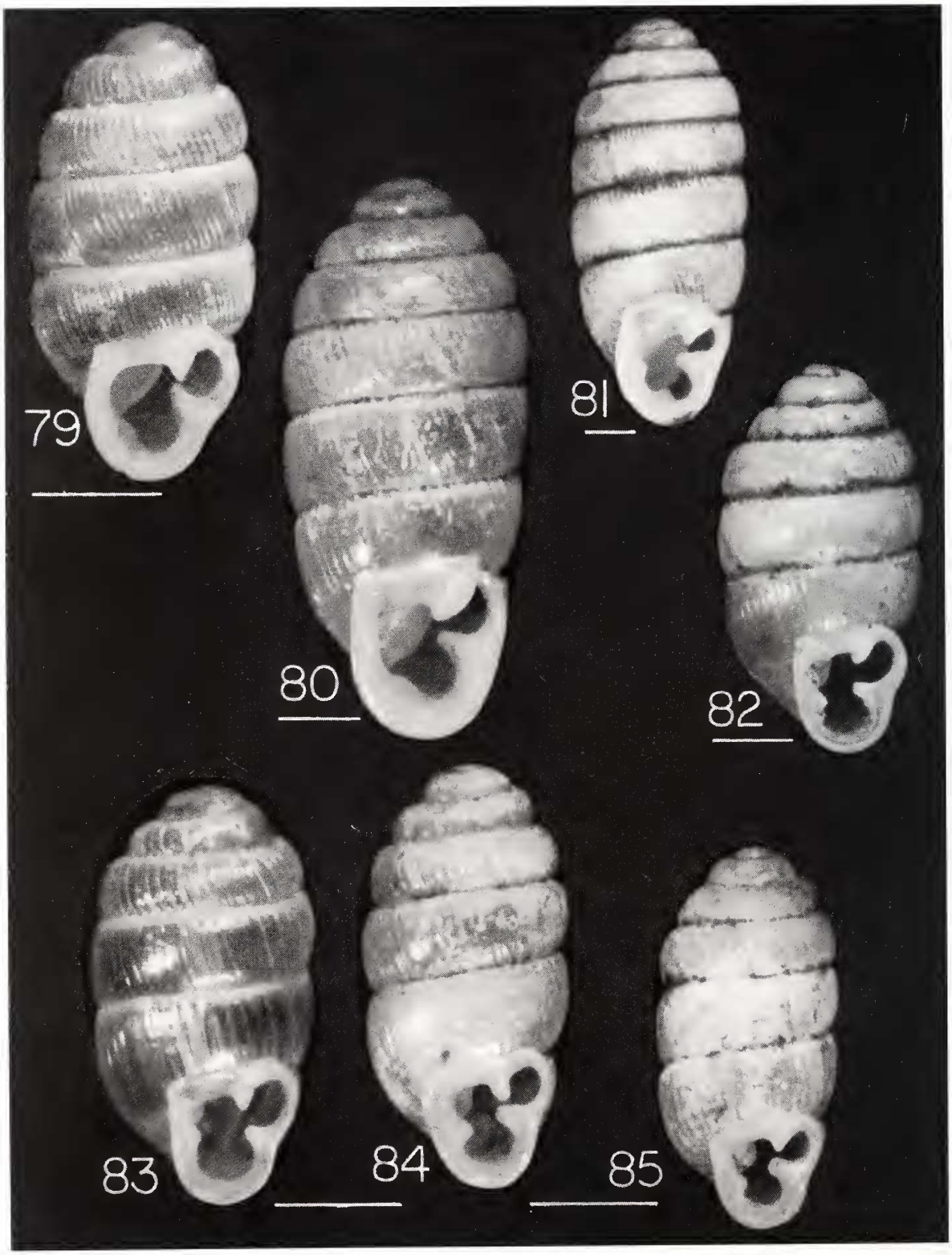
Station	#Sn	Wh/lnHt	D1st1.5Wh
1389	1ad,1juv	3.99	0.98-1.01
1391	1	4.06	0.92

ETYMOLOGY. For Fotobohitra, the type locality.

Gulella razafyi sp. nov.
Fig. 23

DIAGNOSIS. *G. razafyi* sp. nov. is somewhat similar to the Comoran *G. oryza* (Morelet, 1882) but is much more loosely coiled. Among Madagascan *Gulella* with (a) apertural dentition restricted to a moderate-sized parietal tooth and a moderate-sized palatal tooth, (b) baso-columellar lamella absent to weak, (c) general rib sculpture absent to weak and inconspicuous, (d) height less than 9 mm, (e) shell with height/diameter 2.6 or less and barreled to slightly columnar, (f) columellar recessed baffle inconspicuous or not visible, (g) palatal tooth elevated, narrow, and triangular or pegged, (h) sutures moderately impressed, (i) embryonic whorls 1.8 to 2.2, and (j) diameter of first 1.5 whorls 0.8 to 1.0 mm, two species are distinguished from *G. reeae, G. miaranoniae* sp. nov., and *G. bebokae* sp. nov. by their looser coiling (whorls/ln height 4.0-4.3 *vs.* 4.4-4.7): *G. razafyi* sp. nov. and *G. fotobohitrae* sp. nov. *G. razafyi* sp. nov. differs from *G. fotobohitrae* sp. nov. in its tighter coiling (whorls/ln height 4.2-4.3 *vs.* 4.0) and smaller initial whorl (diameter of first 1.5 whorls 0.84 mm *vs.* 0.92-1.01 mm).

HOLOTYPE. Station 1549 (UF 274986, 1 ad): 17°54'S, 49°12'E: Madagascar: Betampona Reserve, 400 m. 16-May-93.



Figs. 79-85. Fig. 79. *Gulella manomboae* sp. nov. holotype, Manombo Reserve. Fig. 80. *G. michellae* sp. nov. holotype, Marojejy Reserve. Fig. 81. *G. mahagaga* sp. nov. holotype, Tsaratanana Reserve. Fig. 82. *G. hafa* sp. nov. holotype, Marojejy Reserve. Figs. 83-84. *G. benjamini s.s.* Emberton and Pearce, 2000 (to same size scale): Fig. 83 holotype, northwest of Fort Dauphin; Fig. 85 specimen, Pic Saint Louis, near Fort Dauphin. Fig 84. *G. benjamini saintelucensis* subsp. nov. (note tight coiling) holotype, Forêt Sainte Luce, north of Fort Dauphin. All scale bars 1 mm.

DESCRIPTION OF HOLOTYPE. Height 4.3 mm, diameter 2.0 mm (H/D 2.2), whorls 6.3 (whorls/ln height 4.28). Apical angle 85°, barreling 0.0%. Sutural depth 5.6%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.2, diameter of first 1.5 whorls 0.84 mm, embryonic sculpture smooth, with a very faint trace of growth wrinkles. Peristome height 1.5 mm, width 1.3 mm (0.6 shell D; peristome H/W 1.1); apertural lip width 0.28 mm (0.21 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); and a small columellar recessed baffle. Umbilicus an extremely minute crevice.

ETYMOLOGY. For Razafy of Betampona Reserve, the collector.

Gulella josephinae sp. nov.
Fig. 24

DIAGNOSIS. Of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent to weak, and (c) rib sculpture strong to moderate, only two species have shell height generally greater than 9 mm due to loose coiling (whorls/ln height 3.2-3.4): *G. josephinae* sp. nov. and *G. soulaiana. G. josephinae* sp. nov. differs from *G. soulaiana* in its looser coiling (whorls/ln height about 3.2 *vs.* about 3.4), the flattened (*vs.* rounded) peripheries of its middle whorls, and its dry-deciduous (*vs.* rainforest) habitat.

HOLOTYPE. Station 61 (UF 274852, 1 ad): 16°23'S, 45°18'E: Madagascar: Namoroka Reserve, 105 m: dry deciduous forest. 25-May-95.

DRY PARATYPES. Stations 61 (UF 274858, 32 ad, 27 juv); 62 (UF 274859, 7 ad, 6 juv); 67 (UF 274860, 5 ad, 1 juv); 68 (UF 274861, 16 ad, 6 juv); 69 (UF 274854, 62 ad, 67 juv; AMS C203585, 3 ad; ANSP 403459, 3 ad; MNHN, 3 ad); 70 (UF 274855, 55 ad, 57 juv); 71 (UF 274856, 1 ad); 72 (UF 274857, 2 ad, 3 juv); 73 (UF 274862, 10 ad, 11 juv); 74 (UF 274853, 60 ad, 46 juv).

ALCOHOL PARATYPES. Stations 61 (UF 275095, 1 ad); 63 (UF 275093, 1 juv); 68 (UF 275098, 1 ad); 69 (UF 275094, 2 ad, 1 juv); 70 (UF 275096, 1 juv); 73 (UF 275092, 1 ad); 74 (UF 275097, 1 juv).

DESCRIPTION OF HOLOTYPE. Height 9.8 mm, diameter 3.7 mm (H/D 2.6), whorls 7.3 (whorls/ln height 3.20). Apical angle 95°, barreling 4.1%. Sutural depth 4.0%, sutural crenulation moderate. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 1.6, diameter of first 1.5 whorls 1.68 mm, embryonic sculpture smooth, with traces of growth lines. Peristome height 2.8 mm, width 2.8 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.63 mm (0.23 peristome W). Apertural barriers consisting of a large parietal tooth; a small, rounded palatal tooth that is buttressed below (parietal-palatal embayment somewhat narrow); and a small columellar recessed baffle. Umbilicus a crevice.

ETYMOLOGY. For Josephine Djaohasara Emberton, wife of the author.

Gulella soulaiana Fischer-Piette in Fischer-Piette, Cauquoin and Testud, 1973
Fischer-Piette *et al.* (1994): plate IV, fig. 19 (holotype)

DIAGNOSIS. Of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent to weak, and (c) rib sculpture strong to moderate, only two species have shell height generally greater than 9 mm due to loose coiling (whorls/ln height 3.2-3.4): *G. soulaiana* and *G. josephinae* sp. nov. *G. soulaiana* differs from *G. josephinae* sp. nov. in its tighter coiling (whorls/ln height about 3.4 *vs.* about 3.2), the rounded (*vs.* flattened) peripheries of its middle whorls, and its rainforest (*vs.* deciduous-forest) habitat.

DESCRIPTION OF HOLOTYPE (based on illustration in Fischer-Piette *et al.*, 1994). Height 10.5 mm, diameter 4.4 mm (H/D 2.4), whorls 8.0 (whorls/ln height 3.40). Apical angle 90°, barreling 5.6%. Sutural depth 5.6%. In apertural view, penultimate and body whorls with strong rib sculpture that does not diminish between upper and lower sutures. Peristome height 3.4 mm, width 2.9 mm (0.7 shell D; peristome H/W 1.2); apertural lip width 0.80 mm (0.28 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, peg-triangular palatal tooth (parietal-palatal embayment fairly wide); and a small columellar recessed baffle. Umbilicus "a miniscule perforation."

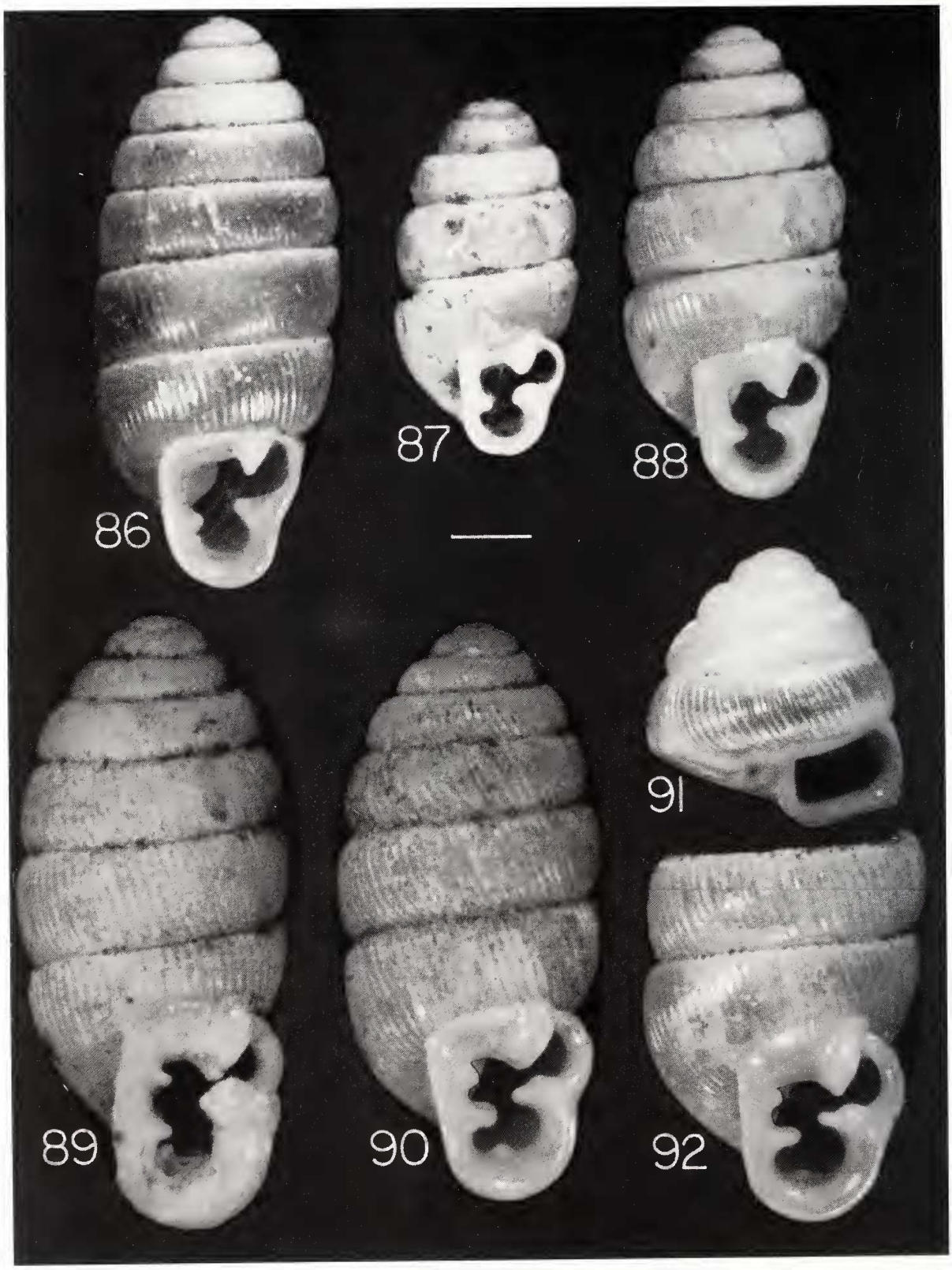
Gulella rugosa sp. nov.
Fig. 25

DIAGNOSIS. *G. rugosa* sp. nov. is somewhat similar to the Comoran *G. spreta* (Morelet, 1883) but has a much blunter apex and is much more loosely coiled. Of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent to weak, and (c) shell height generally less than 7.5 mm due to tight coiling (whorls/ln height 3.7-4.4), only two species have very strong and high-standing rib sculpture: *G. rugosa* sp. nov. and *G. columna* sp. nov. *G. rugosa* sp. nov. differs from *G. columna* sp. nov. in its much looser coiling (whorls/ln height about 3.7 *vs.* about 4.1) and larger initial whorl (diameter of first 1.5 whorls about 1.0 mm *vs.* about 0.8 mm).

HOLOTYPE. Station 814 (UF 274987, 1 ad): 12°56'S, 49°07'E: Madagascar: Ankarana Reserve, 70 m. 11-Oct-94.

DRY PARATYPES. Station 814 (UF 274988, 1 juv; AMS C203611, 1 ad, 1 juv; MNHN, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 7.2 mm, diameter 2.7 mm (H/D 2.7), whorls 7.4 (whorls/ln height 3.74). Apical angle 90°, barreling -2.4%. Sutural depth 2.4%,



Figs. 86-92. Figs. 86-88. *Gulella mahafinaratra* sp. nov.: Fig. 86 holotype, east of Marojejy Reserve; Figs. 87, 88 paratypes, Marojejy Reserve. Figs. 89-92. *G. hafahafa* sp. nov.: Fig. 89 holotype, south of Mananara; Fig. 90 paratype, Isle Sainte Marie; Figs. 91-92 paratypes, Betampona Reserve. Scale bar 1 mm.

sutural crenulation moderate. In apertural view, penultimate and body whorls with very strong rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls estimated at 1.7, diameter of first 1.5 whorls 1.00 mm, embryonic sculpture smooth, with a faint trace of growth lines or riblets. Peristome height 2.3 mm, width 2.1 mm (0.8 shell D; peristome H/W 1.1); apertural lip width 0.41 mm (0.19 peristome W). Apertural barriers consisting of a large parietal tooth; a moderate, broadly rounded palatal tooth (parietal-palatal embayment somewhat narrow); and a small columellar recessed baffle. Umbilicus a crevice.

ETYMOLOGY. For the coarsely ribbed, or wrinkled (Latin "rugosa") sculpture.

Gulella columna sp. nov.
Fig. 26

DIAGNOSIS. *G. columna* sp. nov. is somewhat similar to the Comoran *G. spreta* (Morelet, 1883) but is more loosely coiled and has a slenderer, more columnar shape. Of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent to weak, and (c) shell height generally less than 7.5 mm due to tight coiling (whorls/ln height 3.7-4.4), only two species have very strong and high-standing rib sculpture: *G. columna* sp. nov. and *G. rugosa* sp. nov. *G. columna* sp. nov. differs from *G. rugosa* sp. nov. in its much tighter coiling (whorls/ln height about 4.1 *vs.* about 3.7) and smaller initial whorl (diameter of first 1.5 whorls about 0.8 mm *vs.* about 1.0 mm).

HOLOTYPE. Station 807 (UF uncatalogued, 1 ad, possibly lost): 12°54'S, 49°06'E: Madagascar: Ankarana Reserve, 90 m. 10-Oct-94.

DRY PARATYPE. Station 807 (AMS C203576, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 6.3 mm, diameter 2.3 mm (H/D 2.8), whorls 7.6 (whorls/ln height 4.13). Apical angle 105°, barreling -1.4%. Sutural depth 12.0%, sutural crenulation moderate. In apertural view, penultimate and body whorls with strong rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 1.6, diameter of first 1.5 whorls 0.84 mm, embryonic sculpture smooth. Peristome height 1.8 mm, width 1.7 mm (0.8 shell D; peristome H/W 1.0); apertural lip width 0.28 mm (0.16 peristome W). Apertural barriers consisting of a large parietal tooth; a large, rounded palatal tooth (parietal-palatal embayment somewhat narrow); and a small columellar recessed baffle. Umbilicus a crevice.

ETYMOLOGY. For the shape and sculpture reminiscent of a Greek architectural column (Latin "columna").

Gulella pearcei sp. nov.
Fig. 27

DIAGNOSIS. *G. pearcei* sp. nov. is somewhat similar to the South African *G. rogersi* (Melvill and Ponsonby, 1898) in apertural morphology, size, and coiling tightness, but is slenderer and less columnar, with a sharper apex; its aperture is proportionally much smaller; and its palatal tooth is bifid instead of undivided. Of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent to weak, and (c) strong to moderate rib sculpture, *G. pearcei* sp. nov. is unique in having its palatal tooth high in position and notched opposite the parietal tooth.

HOLOTYPE. Station 222 (UF 274971, 1 ad): 12°19'S, 49°20'E: Madagascar: Montagne des Français, 230 m: dry deciduous forest, 21-Jul-95.

DESCRIPTION OF HOLOTYPE. Height 5.3 mm, diameter 2.4 mm (H/D 2.2), whorls 7.6 (whorls/ln height 4.55). Apical angle 100°, barreling 7.9%. Sutural depth 15.4%, sutural crenulation weak. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 2.1, diameter of first 1.5 whorls 0.93 mm, embryonic sculpture smooth. Peristome height 1.1 mm, width 0.9 mm (0.4 shell D; peristome H/W 1.2); apertural lip width 0.19 mm (0.21 peristome W). Apertural barriers consisting of a large parietal tooth; a very large palatal tooth, notched opposite the parietal tooth; (parietal-palatal embayment wide); and a moderate, deep columellar recessed baffle. Umbilicus minute.

ETYMOLOGY. For Dr. Tim Pearce, in grateful recognition of his outstanding contributions as postdoctoral associate during 1995 fieldwork and 1996 lab work.

Gulella tsaratananae sp. nov.
Figs. 27, 28

DIAGNOSIS. *G. tsaratananae* sp. nov. is somewhat similar to the Comoran *G. spreta* (Morelet, 1883) but is more loosely coiled and has a blunter apex. *G. tsaratananae* sp. nov. bears some resemblance to the Comoran *G. oryza* (Morelet, 1882) but is much more loosely coiled. *G. tsaratananae* sp. nov. is also somewhat similar to the West African *G. sulcifera* (Morelet, 1883) but is more tightly coiled and has larger apertural teeth. Two species of Madagascan *Gulella* have (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent to weak, (c) moderately strong and low-standing rib sculpture, (d) shell height generally less than 7.5 mm due to tight coiling (whorls/ln height 4.1-4.4), and (e) palatal tooth medial in position and unnotched: *G. tsaratananae* sp. nov. and *G. miaryi*. *G. tsaratananae* sp. nov. differs from *G. miaryi* in its looser coiling (whorls/ln height about 4.1 *vs.* about 4.4) and its rainforest (*vs.* dry forest) habitat.

HOLOTYPE. Station 108 (UF 275008, 1 ad): 14°01'S, 48°46'E: Madagascar: Tsaratanana Reserve, 630 m: rainforest. 17-Jun-95.

Figs. 93-97. Fig. 93. *Gulella vatosoa* sp. nov. holotype, western Masoala Peninsula. Figs. 94-97. *G. vakinifia* sp. nov.: Fig. 94 holotype, southern Bemaraha Reserve; Figs. 95-97 paratypes: Fig. 95 type locality; Fig. 96 Namoroka Reserve; Fig. 97 northern Bemaraha Reserve. Scale bar 1 mm.

FIGURED PARATYPE. Station 105 (UF 275009, 1 ad).
OTHER DRY PARATYPES. Stations 95 (UF 275017, 1 juv); 105 (UF 275021, 3 ad); 106 (13 ad, specimens lost); 107 (UF 275011, 1 ad); 108 (UF 275018, 8 ad, 2 juv; AMS C203615, 2 ad; ANSP 403460, 2 ad; MNHN, 2 ad); 110 (UF 275013, 9 ad, 2 juv); 111 (UF 275015, 3 ad, 1 juv); 112 (UF 275014, 9 ad, 1 juv); 114 (UF 275019, 9 ad, 1 juv); 502 (UF 275010, 1 ad, 1 juv); 503 (UF 275016, 13 ad, 6 juv); 537 (UF 275012, 1 ad); 538 (UF 275020, 2 ad); 540 (UF 275022, 4 ad, 2 juv).
ALCOHOL PARATYPES. Stations 105 (UF 275148, 2 ad, 1 juv); 106 (UF 275143, 2 ad); 108 (UF 275147, 9 ad); 110 (UF 275146, 2 ad); 112 (UF 275144, 2 ad); 114 (UF 275145, 2 ad, 1 juv); 115 (UF 275149, 1 ad); 540 (UF 275142, 2 ad).
DESCRIPTION OF HOLOTYPE. Height 5.6 mm, diameter 2.3 mm (H/D 2.4), whorls 7.1 (whorls/ln height 4.14). Apical angle 80°, barreling -2.7%. Sutural depth 5.6%, sutural crenulation strong. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.85 mm, embryonic sculpture smooth, with a possible faint trace of minute riblets. Peristome height 1.6 mm, width 1.7 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.23 mm (0.14 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); and a small columellar recessed baffle. Umbilicus a crevice.
ETYMOLOGY. For Tsaratanana Reserve.

Gulella miaryi Fischer-Piette and Bedoucha, 1964
Fischer-Piette *et al.* (1994): fig. 54

DIAGNOSIS. Two species of Madagascan *Gulella* have (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella absent to weak, (c) moderately strong and low-standing rib sculpture, (d) shell height generally less than 7.5 mm due to tight coiling (whorls/ln height 4.1-4.4), and (e) palatal tooth medial in position and unnotched: *G. miaryi* and *G. tsaratananae* sp. nov. *G. miaryi* differs from *G. tsaratananae* sp. nov. in its tighter coiling (whorls/ln height about 4.4 *vs.* about 4.1) and its dry forest (*vs.* rainforest) habitat.
DESCRIPTION OF HOLOTYPE (based on illustration in Fischer-Piette *et al.*, 1994). Height 5.0 mm, diameter 2.1 mm (H/D 2.4), whorls 7.0 (whorls/ln height 4.35). Apical angle 105°, barreling 3.4%. Sutural depth 5.3%, sutural crenulation moderate. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Peristome height 1.7 mm, width 1.6 mm (0.8 shell D; peristome H/W 1.1); apertural lip width 0.30 mm (0.16 peristome W). Apertural barriers consisting of a large parietal tooth; a moderate, peg-triangular palatal tooth (parietal-palatal embayment fairly wide); and a small columellar recessed baffle. Umbilicus imperforate, apparently.

Gulella zanahary sp. nov.
Fig. 29

DIAGNOSIS. Of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, and (c) general rib sculpture weak to none, *G. zanahary* sp. nov. is unique in having its (a) columellar recessed baffle huge, (b) pre-apertural base angular in profile, and (c) palatal tooth massive and often with deeply internal outlier. *G. zanahary* sp. nov. is also unique in these characters among Madagascan *Gulella* having (a) smooth penultimate-whorl and upper-whorl sculpture; (b) apertural dentition consisting of parietal, palatal teeth, and baso-columellar teeth; (c) baso-columellar tooth buttressed equally above and below; (d) whorls/ln height 4.0-4.4; and (e) diameter of first 1.5 whorls 0.9-1.0 mm.
HOLOTYPE. Station 238 (UF 275056, 1 ad): 12°00'S, 49°17'E: Madagascar: Cap d'Ambre, near Ambatojanahary, 40 m: baobab-deciduous forest. 25-Jul-95.
FIGURED PARATYPES. Stations 241 (UF 275058, 1 ad); 407 (UF 275057, 1 ad).
OTHER DRY PARATYPES. Stations 238 (UF 275064, 4 ad, 14 juv); 239 (UF 275059, 11 ad, 2 juv; AMS C203623, 1 ad; ANSP 403461, 1 ad; MNHN, 1 ad); 400 (UF 275062, 4 ad); 404 (UF uncatalogued, 2 ad, 1 juv, possibly lost); 405 (UF 275061, 4 ad, 1 juv); 407 (UF 275063, 2 ad, 1 juv).
ALCOHOL PARATYPES. Station 238 (UF 275168, 7 ad).
DESCRIPTION OF HOLOTYPE. Height 6.9 mm, diameter 2.6 mm (H/D 2.7), whorls 8.3 (whorls/ln height 4.28). Apical angle 105°, barreling 2.4%. Sutural depth 3.6%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.93 mm, embryonic sculpture smooth. Peristome height 2.1 mm, width 1.8 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.38 mm (0.20 peristome W). Pre-apertural base of shell angular in profile. Apertural barriers consisting of a massive parietal tooth; a very large, curved-triangular palatal tooth that has a deeply internal outlier (parietal-palatal embayment fairly narrow, nearly enclosed); a massive columellar recessed baffle; and a strong, recessed baso-columellar lamella. Umbilicus a small crevice.
VARIATION. See Tables 2, 3. A baso-columellar tooth is sometimes present (Figs. 79, 80).
ETYMOLOGY. For its type locality, near Ambatojanahary (Malagasy "place of the rock of God").

Gulella lohabea sp. nov.
Fig. 30

DIAGNOSIS. Of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, (c) general rib sculpture weak to none, *G. lohabea* sp. nov. is unique in its large initial whorl (diameter of first 1.5 whorls about 1.3 mm *vs.* 0.8-1.1 mm) and its transverse (*vs.* spirally lamellar

to nodular) palatal tooth, and is rare in having its parietal tooth joined to and continuous with the apertural lip. *G. lohabea* sp. nov. resembles *G. boucheti*, but differs in its presence (*vs.* absence) of a baso-columellar lamella and in its smaller initial whorl (diameter of first 1.5 whorls 1.28 mm *vs.* 1.35-1.36 mm).

HOLOTYPE. Station 201 (UF 274877, 1 ad): 12°44'S, 49°30'E: Madagascar: Analamera Reserve, 315 m: dry deciduous forest. 15-Jul-95.

DRY PARATYPES. Station 201 (UF 274878, 28 ad, 8 juv; AMS C203588, 1 ad; ANSP 403462, 1 ad; MNHN, 1 ad).

ALCOHOL PARATYPES. Station 201 (UF 273598, 6 ad, 3 juv).

DESCRIPTION OF HOLOTYPE. Height 6.4 mm, diameter 2.7 mm (H/D 2.4), whorls 7.1 (whorls/ln height 3.81). Apical angle 105°, barreling 8.1%. Sutural depth 4.7%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.7, diameter of first 1.5 whorls 1.28 mm, embryonic sculpture of faint growth lines and very faint spiral striae. Peristome height 2.0 mm, width 1.9 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.34 mm (0.18 peristome W). Apertural barriers consisting of a moderate parietal tooth that is joined to and continuous with the apertural lip; a moderate, transverse, broad, rounded palatal tooth (parietal-palatal embayment somewhat narrow); a small columellar recessed baffle; and a moderate baso-columellar lamella. Umbilicus a minute, very narrow crevice.

ETYMOLOGY. For the enlarged apex (Malagasy "loha" = head, "be" = big).

Gulella ankaranensis Fischer-Piette, Blanc, Blanc and Salvat, 1994
Fischer-Piette *et al.* (1994): figs. 60 (holotype) and 61-62 (paratypes)
Fig. 31 (specimen)

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, and (c) general rib sculpture weak to none, *G. ankaranensis* is unique in its very tight coiling (whorls/ln height 5.0-5.2) and very small initial whorl (diameter of first 1.5 whorls 0.75-0.79 mm). To avoid misidentification of *G. ankaranensis* as the similar and sometimes sympatric *G. fischerpiettei* sp. nov. or *G. satisfacta*, coiling tightness and initial whorl size must be checked carefully.

FIGURED SPECIMEN. Station 558 (UF 274767, 1 ad).

OTHER DRY VOUCHER SPECIMENS. Stations 554 (UF 274768, 1 ad); 558 (UF 274770, 2 ad); 561 (UF 274773, 1 ad); 564 (UF 274772, 1 ad, 1 juv); 565 (UF 274771, 1 ad); 568 (UF 274775, 3 ad); 570 (UF 274774, 1 ad, 2 juv); 571 (UF 274769, 2 ad, 1 juv; AMS C203567, 1 ad; ANSP 403463, 1 ad; MNHN, 1 ad).

DESCRIPTION OF HOLOTYPE (based on illustration in Fischer-Piette *et al.*, 1994). Height 4.0 mm, diameter 1.5 mm (H/D 2.7), whorls 7.0 (whorls/ln height 5.05). Apical angle 90°, barreling 2.0%. Sutural depth 3.8%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Peristome height 0.9 mm, width 1.1 mm (0.8 shell D; peristome H/W 0.8); apertural lip width 0.20 mm (0.16 peristome W). Apertural barriers consisting of a large parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment fairly narrow); a small columellar recessed baffle; and a moderate baso-columellar lamella.

VARIATION. See Table 2.

Gulella fischerpiettei sp. nov.
Fig. 32

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, and (c) general rib sculpture weak to none, *G. fischerpiettei* sp. nov. is intermediate between and disjunct from *G. ankaranensis* and *G. satisfacta* in both coiling tightness (whorls/ln height 4.6-4.8, *vs.* 5.0-5.2 and 4.1-4.3) and initial whorl size (diameter of first 1.5 whorls 0.80-0.90 mm, *vs.* 0.75-0.79 mm and 0.91-0.96 mm). *G. fischerpiettei* sp. nov. is otherwise very similar to both these species, and is sometimes sympatric with each. *G. fischerpiettei* sp. nov. may have a broadish, somewhat indistinct baso-columellar tooth; it then differs from other species of similar dentition in its coiling tightness and its small-to-moderate columellar recessed baffle.

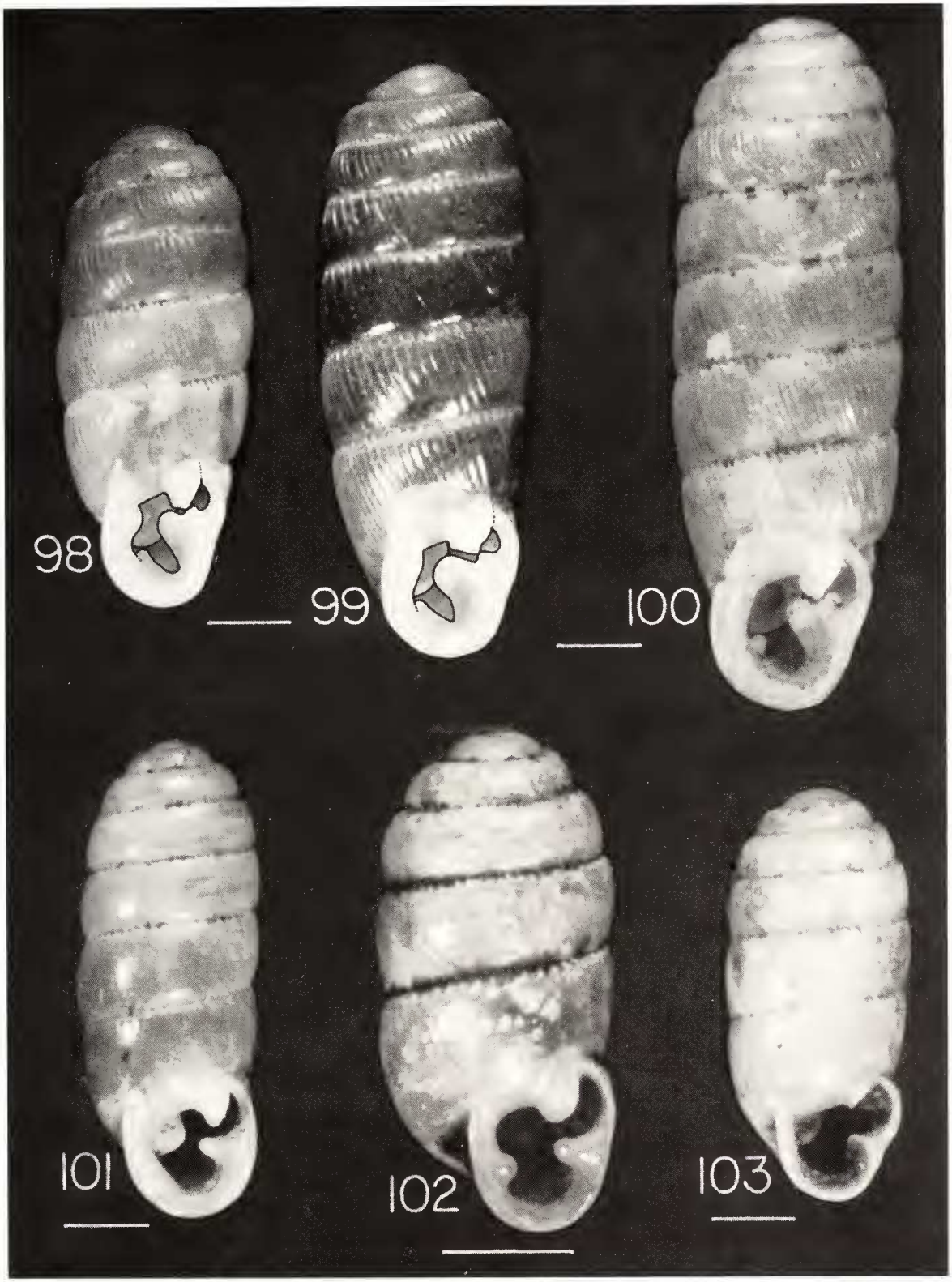
HOLOTYPE. Station 558 (UF 274824, 1 ad): 12°54'S, 49°06'E: Madagascar: Ankarana Reserve, 80 m: dry deciduous forest. 22-Aug-95.

DRY PARATYPES. Stations 558 (UF 274825, 3 ad); 803 (UF 274826, 2 ad).

DESCRIPTION OF HOLOTYPE. Height 4.7 mm, diameter 1.8 mm (H/D 2.6), whorls 7.3 (whorls/ln height 4.69). Apical angle 115°, barreling 1.1%. Sutural depth 5.6%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.9, diameter of first 1.5 whorls 0.90 mm, embryonic sculpture smooth. Peristome height 1.2 mm, width 1.2 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.20 mm (0.16 peristome W). Apertural barriers consisting of a moderate parietal tooth that is separated by a groove from the apertural lip; a large, triangular palatal tooth that is nub-like and slightly recessed (parietal-palatal embayment moderately wide); a small columellar recessed baffle; and a moderate baso-columellar lamella. Umbilicus imperforate.

VARIATION. See Tables 2, 3, 4.

ETYMOLOGY. For the late E. Fischer-Piette, monographer of the Madagascan land-snail fauna.



Figs. 98-103. Figs. 98, 99. *Gulella orchida* sp. nov.: Fig. 98 holotype, Montagne des Orchides; Fig. 99 paratype, Montagne des Français. Fig. 100. *G. magnorchida* sp. nov. holotype, southern Cap d'Ambre. Fig. 101. *G. mahia* sp. nov. paratype, northern Cap d'Ambre. Fig. 102. *G. nosybei* sp. nov. paratype, Nosy Komba. Fig. 103. *G. ambanikelia* sp. nov. neoadult paratype, type locality, Ankarana Reserve. All scale bars 1 mm.

Gulella fischerpiettei enigma subsp. nov.
Fig. 33

DIAGNOSIS. Differs from *G. fischerpiettei s.s.* sp. nov. in its smaller initial whorl (diameter of first 1.5 whorls 0.80-0.84 mm vs. 0.86-0.90 mm), its palatal tooth that is spirally lamellar and not recessed (*vs.* nub-like and slightly recessed), and its parietal tooth that is continuous with the apertural lip (*vs.* separated by a groove from the apertural lip).

HOLOTYPE. Station 816 (UF 274827, 1 ad): 12°55'S, 49°03'E: Madagascar: Ankarana Reserve, 100 m. 12-Oct-94.

DRY PARATYPES. Station 815 (UF 274828, 7 ad).

DESCRIPTION OF HOLOTYPE. Height 4.0 mm, diameter 1.7 mm (H/D 2.3), whorls 6.4 (whorls/ln height 4.58). Apical angle 90°, barreling 3.3%. Sutural depth 3.3%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.80 mm, embryonic sculpture smooth. Peristome height 1.3 mm, width 1.3 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.30 mm (0.23 peristome W). Apertural barriers consisting of a large parietal tooth that is continuous with the apertural lip; a large, triangular palatal tooth that is spirally lamellar and not recessed (parietal-palatal embayment moderately wide); a moderate columellar recessed baffle; a moderate baso-columellar lamella; and a weak baso-columellar tooth. Umbilicus a crevice.

VARIATION. See Table 4.

ETYMOLOGY. For the enigmatic size and shape, which superficially resembles an enlarged *Gulella ankaranensis*.

Gulella satisfacta Fischer-Piette, Blanc, Blanc and Salvat, 1994
Figs. 36, 37, 38

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, and (c) general rib sculpture weak to none, *G. satisfacta* is unique in its combination of (a) broadly rounded, non-tooth-like columellar recessed baffle; (b) diameter of first 1.5 whorls 0.91-0.96; and (c) whorls/ln height 4.09-4.30. *G. satisfacta* is not known outside Ankarana Reserve and adjacent karst, where it is sometimes sympatric with either *G. ankaranensis* or *G. fischerpiettei* sp. nov. It shares its broadly rounded, non-tooth-like columellar recessed baffle with these two species, but differs from them in its looser coiling (whorls/ln height 4.09-4.30 *vs.* 4.6-5.2) and larger initial whorl (diameter of first 1.5 whorls 0.91-0.96 *vs.* 0.75-0.90 mm). Three species of southern Cap d'Ambre (*G. mahia* sp. nov., *G. ranomasina* sp. nov., and *G. jaominai* sp. nov.) can overlap or approach *G. satisfacta* in coiling tightness and/or initial-whorl size, but differ from it in their nubbed, toothlike columellar recessed baffles.

FIGURED SPECIMENS. Stations 564 (UF 274993, 1 ad); 576 (UF 274991, 1 ad); 577 (UF 274992, 1 ad).

OTHER DRY VOUCHER SPECIMENS. Stations 564 (UF 274995, 12 ad, 4 juv); 570 (UF 274994, 2 juv); 576 (UF 274997, 2 ad, 1 juv); 577 (UF 274996, 5 ad, 1 juv).

ALCOHOL VOUCHER SPECIMENS. Station 564 (UF 275139, 2 ad, 1 juv).

DESCRIPTION OF HOLOTYPE (based on illustration in Fischer-Piette *et al.*, 1994). Height 6.2 mm, diameter 2.4 mm (H/D 2.6), whorls 7.5 (whorls/ln height 4.11). Apical angle 80o, barreling 7.6%. Sutural depth 7.8%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Peristome height 1.5 mm, width 1.7 mm (0.7 shell D; peristome H/W 0.9); apertural lip width 0.21 mm (0.12 peristome W). Apertural barriers consisting of a large parietal tooth; a large, rounded-triangular palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; and a strong baso-columellar lamella.

VARIATION. See Tables 2, 3, 4.

Gulella satisfacta charlesblanci subsp. nov.
Fig. 34

DIAGNOSIS. Differs from both *G. satisfacta s.s.* and *G. s. vitsia* subsp. nov. in its tighter coiling (whorls/ln height 4.30 *vs.* 4.09-4.21) and its presence (*vs.* absence) of a small baso-columellar tooth. It further differs from *G. s. vitsia* subsp. nov. in its smooth (*vs.* weakly ribbed) sculpture and its large (*vs.* extremely large) baso-columellar lamella. *G. s. charlesblanci* subsp. nov. differs from other species of similar, tridentate dentition in its coiling tightness and its small-to-moderate columellar recessed baffle.

HOLOTYPE. Station 571 (UF 274989, 1 ad): 12°57'S, 49°07'E: Madagascar: Ankarana Reserve, 85 m: dry deciduous forest. 24-Aug-95.

DESCRIPTION OF HOLOTYPE. Height 4.8 mm, diameter 1.8 mm (H/D 2.6), whorls 6.7 (whorls/ln height 4.30). Apical angle 85°, barreling 4.2%. Sutural depth 8.5%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Diameter of first 1.5 whorls 0.95 mm. Peristome height 1.3 mm, width 1.3 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.28 mm (0.19 peristome W). Apertural barriers consisting of a large parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; a strong baso-columellar lamella; and a weak baso-columellar tooth.

ETYMOLOGY. For Charles P. Blanc, co-monographer of Madagascan land snails.

Gulella satisfacta vitsia subsp. nov.
Fig. 35

DIAGNOSIS. Differs from both *G. satisfacta s.s.* and *G. s.*

charlesblanci subsp. nov. in its weakly ribbed (*vs.* smooth) sculpture and its baso-columellar lamella that is massive and extends upward to near the columellar insertion (*vs.* strong but not approaching the columellar insertion). Further differs from *G. s. charlesblanci* subsp. nov. in its looser coiling (whorls/ln height 4.09-4.21 vs. 4.30) and its absence (*vs.* presence) of a small baso-columellar tooth.

HOLOTYPE. Station 810 (UF 274998, 1 ad): 12°54'S, 49°06'E: Madagascar: Ankarana Reserve, 90 m. 10-Oct-94.

ALCOHOL PARATYPE. Station 810 (UF 275140, 1 ad)

DESCRIPTION OF HOLOTYPE. Height 5.1 mm, diameter 1.9 mm (H/D 2.7), whorls 6.8 (whorls/ln height 4.18). Apical angle 100°, barreling 1.7%. Sutural depth 6.5%, sutural crenulation strong. In apertural view, penultimate and body whorls with weak rib sculpture that does not diminish in strength toward the lower suture. Embryonic whorls 2.1, diameter of first 1.5 whorls 0.95 mm, embryonic sculpture smooth. Peristome height 1.6 mm, width 1.4 mm (0.8 shell D; peristome H/W 1.1); apertural lip width 0.23 mm (0.16 peristome W). Apertural barriers consisting of a large parietal tooth; a large, rounded-triangular palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; and a very strong baso-columellar lamella, extending upward to near the columellar insertion. Umbilicus a crevice.

ETYMOLOGY. For the seeming rarity (Malagasy "vitsy" = rare) of the taxon, known from a single specimen.

Gulella mahia sp. nov.
Figs. 39, 40, 101

DIAGNOSIS. There are three species of Madagascan Gulella having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, (c) general rib sculpture weak to none, (d) whorls/ln height 3.9-4.4, (e) diameter of first 1.5 whorls 0.88-1.02 mm, and (e) columellar recessed baffle nubbed and tooth-like: *G. mahia* sp. nov., *G. ranomasina* sp. nov., and *G. jaominai* sp. nov. *G. mahia* sp. nov. differs from the latter two in its larger initial whorl (diameter of first 1.5 whorls 0.98-1.02 mm *vs.* 0.88-0.93 mm) and its intermediate coiling tightness (whorls/ln height 4.1 *vs.* 4.2-4.4 and 3.9-4.0). *G. mahia* sp. nov. is sometimes sympatric with *G. ranomasina* sp. nov., from which it further differs in the convex (*vs.* concave) sides of its shell. *G. mahia* sp. nov. differs from *G. satisfacta* in its nubbed and toothlike (*vs.* broadly rounded and non-toothlike) baso-columellar lamella and in its larger initial whorl size (diameter of first 1.5 whorls 0.975-1.025 mm *vs.* 0.913-0.962 mm).

HOLOTYPE. Station 400 (UF 274902, 1 ad): 12°10'S, 49°13'E: Madagascar: Cap d'Ambre, la Butte Bobaomby, 70 m: dry deciduous forest. 24-Aug-95.

FIGURED PARATYPES. Stations 239 (UF 274904, 1 ad); 400 (UF 274903, 1 ad).

OTHER DRY PARATYPES. Stations 400 (UF 274905, 1 juv); 403 (AMS C203595, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 5.0 mm, diameter 2.1 mm (H/D 2.4), whorls 6.6 (whorls/ln height 4.09). Apical angle 90°, barreling 4.5%. Sutural depth 4.5%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.9, diameter of first 1.5 whorls 0.99 mm, embryonic sculpture smooth. Peristome height 1.4 mm, width 1.5 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.25 mm (0.17 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a moderate, triangular columellar recessed baffle; and a moderate baso-columellar lamella. Umbilicus an extremely minute crevice.

VARIATION. See Table 2.

ETYMOLOGY. For its shape, which superficially resembles an emaciated (Malagasy "mahia") version of *Gulella ambrensis capdambri* subsp. nov., with which it is sometimes sympatric.

Gulella ranomasina sp. nov.
Fig. 41

DIAGNOSIS. There are three species of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, (c) general rib sculpture weak to none, (d) whorls/ln height 3.9-4.4, (e) diameter of first 1.5 whorls 0.88-1.02 mm, and (e) columellar recessed baffle nubbed and tooth-like: *G. ranomasina* sp. nov., *G. jaominai* sp. nov., and *G. mahia* sp. nov. *G. ranomasina* sp. nov. differs from the latter two in the concave (*vs.* convex) sides of its shell, and further differs from *G. jaominai* sp. nov. in its tighter coiling (whorls/ln height 4.22-4.40 *vs.* 3.90-3.98). *G. ranomasina* sp. nov. is sometimes sympatric with *G. mahia* sp. nov., from which it further differs in both its smaller initial whorl (diameter of first 1.5 whorls 0.875-0.932 mm *vs.* 0.975-1.025 mm) and its tighter coiling (whorls/ln height 4.22-4.40 *vs.* 4.07-4.12). *G. ranomasina* sp. nov. differs from *G. satisfacta* in its nubbed and toothlike (*vs.* broadly rounded and non-toothlike) baso-columellar lamella and in its concave-sided shell.

HOLOTYPE. Station 241 (UF 274982, 1 ad): 12°00'S, 49°17'E: Madagascar: Cap d'Ambre, near Ambatojanahary, 15 m: dry deciduous forest. 25-Jul-95.

DRY PARATYPES. Stations 238 (UF 274983, 8 ad, 2 juv; AMS C203609, 1 ad; ANSP 403464, 1 ad; MNHN, 1 ad); 239 (UF 274984, 3 ad, 1 juv); 240 (UF 274985, 3 ad).

ALCOHOL PARATYPES. Stations 239 (UF 275138, 1 ad); 240 (UF 275137, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 5.3 mm, diameter 1.8 mm (H/D 2.9), whorls 7.2 (whorls/ln height 4.31).

Apical angle 95°, barreling 0.0%. Sutural depth 6.7%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.8, diameter of first 1.5 whorls 0.88 mm, embryonic sculpture smooth. Peristome height 1.5 mm, width 1.4 mm (0.8 shell D; peristome H/W 1.1); apertural lip width 0.25 mm (0.18 peristome W). Apertural barriers consisting of a large parietal tooth; a moderate, peg-shaped palatal tooth with a broad triangular base (parietal-palatal embayment somewhat narrow); a moderate, nubbed columellar recessed baffle; and a moderate baso-columellar lamella. Umbilicus an extremely small crevice.

VARIATION. See Table 2.

ETYMOLOGY. For the ocean water (Malagasy "ranomasina") near the type locality.

Gulella jaominai sp. nov.
Fig. 42

DIAGNOSIS. There are three species of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, (c) general rib sculpture weak to none, (d) whorls/ln height 3.9-4.4, (e) diameter of first 1.5 whorls 0.88-1.02 mm, and (e) columellar recessed baffle nubbed and tooth-like: *G. jaominai* sp. nov., *G. ranomasina* sp. nov., and *G. mahia* sp. nov. *G. jaominai* sp. nov. differs from *G. ranomasina* sp. nov. in its looser coiling (whorls/ln height 3.90-3.98 *vs.* 4.22-4.40) and its straight- to convex-sided (*vs.* concave-sided) shell. *G. jaominai* sp. nov. differs from *G. mahia* in its smaller initial whorl (diameter of first 1.5 whorls 0.91-0.94 mm *vs.* 0.98-1.02 mm) and its looser coiling (whorls/ln height 3.90-3.98 *vs.* 4.07-4.12). *G. jaominai* sp. nov. differs from *G. satisfacta* in its nubbed and toothlike (*vs.* broadly rounded and non-toothlike) baso-columellar lamella and in its looser coiling (whorls/ln height 3.90-3.98 *vs.* 4.09-4.30).

HOLOTYPE. Station 401 (UF 274849, 1 ad): 12°11'S, 49°13'E: Madagascar: Cap d'Ambre, la Butte Bobaomby, 205 m: dry deciduous-baobab forest. 24-Aug-95.

DRY PARATYPES. Stations 401 (UF 274850, 1 ad, 2 juv); 404 (UF 274851, 4 ad, 4 juv).

ALCOHOL PARATYPES. Station 404 (UF 275068, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 6.1 mm, diameter 2.4 mm (H/D 2.5), whorls 7.1 (whorls/ln height 3.94). Apical angle 110°, barreling 1.6%. Sutural depth 8.4%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.94 mm, embryonic sculpture smooth. Peristome height 1.7 mm, width 1.7 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.36 mm (0.21 peristome W). Apertural barriers consisting of a large parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a moderate columellar recessed baffle; and a strong baso-columellar lamella. Umbilicus a crevice.

VARIATION. See Table 2.

ETYMOLOGY. For Jaomina, teacher in Diego Suarez, uncle of the author, and co-collector of this species.

Gulella ambrensis sp. nov.
Fig. 43

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, (c) general rib sculpture weak to none, and (d) palatal tooth spirally lamellar to nodular, *G. ambrensis* sp. nov. is unique in its combination of loose coiling (whorls/ln height 3.68-3.98) and large initial whorl (diameter of first 1.5 whorls 1.02-1.17 mm). Within this group, its coiling is approached only by *G. jaominai* sp. nov. (whorls/ln height 3.90-3.98), which has a much smaller initial whorl (diameter of first 1.5 whorls 0.912-0.938 mm); and its large initial whorl is approached only by *G. mahia* sp. nov., which has tighter coiling (whorls/ln height 4.07-4.12).

HOLOTYPE. Station 181 (UF 274659, 1 ad): 12°37'S, 49°10'E: Madagascar: Montagne d'Ambre National Park, 1040 m: rainforest. 9-Jul-95.

DRY PARATYPES. Stations 170 (UF 274667, 12 ad, 1 juv); 172 (UF 274665, 11 ad, 1 juv); 178 (UF 274666, 1 ad); 181 (UF 274660, 12 ad, 4 juv; AMS C203564, 1 ad; ANSP 403465, 1 ad; MNHN, 1 ad); 182 (UF 274664, 2 ad, 2 juv); 184 (UF 274668, 1 ad); 185 (UF 274662, 3 ad); 192 (UF 274663, 6 ad, 1 juv); 193 (UF 274661, 1 ad); 195 (UF 274669, 41 ad, 9 juv).

ALCOHOL PARATYPES. Stations 172 (UF 273663, 1 ad, 1 juv); 178 (UF 273658, 1 ad); 181 (UF 273662, 6 ad, 1 juv); 182 (UF 273661, 2 ad, 1 juv); 192 (UF 273664, 2 juv); 193 (UF 273659, 1 juv); 195 (UF 273655, 6 ad, 1 juv).

DESCRIPTION OF HOLOTYPE. Height 6.3 mm, diameter 2.8 mm (H/D 2.3), whorls 7.1 (whorls/ln height 3.81). Apical angle 105°, barreling 3.5%. Sutural depth 3.6%, sutural crenulation weak. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.9, diameter of first 1.5 whorls 1.04 mm, embryonic sculpture virtually smooth. Peristome height 2.0 mm, width 1.9 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.34 mm (0.18 peristome W). Apertural barriers consisting of a moderate parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment moderately wide); a moderate, nubbed columellar recessed baffle; and a strong baso-columellar lamella. Umbilicus a crevice.

VARIATION. See Tables 3, 4.

ETYMOLOGY. For Montagne d'Ambre National Park.

Gulella ambrensis andavakoerae subsp. nov.
Fig. 44

DIAGNOSIS. Known only from the Andavakoera massif,

north of Betsiaka. Differs from *G. ambrensis s.s.* sp. nov. in its larger initial whorl (diameter of first 1.5 whorls 1.075-1.100 mm *vs.* 1.025-1.050 mm), strong (*vs.* weak) sutural crenulation, deciduous-forest (*vs.* rainforest) habitat, and extension of the palatal-tooth lamella all the way to (*vs.* stopping before) the apertural-lip edge. Differs from *G. a. capdambri* subsp. nov. in its non-recessed (*vs.* often recessed) palatal tooth and in the extension of its palatal-tooth lamella all the way to (*vs.* stopping before) the apertural-lip edge. Differs from *G. a. orangea* subsp. nov. in its larger initial whorl (diameter of first 1.5 whorls 1.075-1.100 mm *vs.* 1.025-1.038 mm) and in the extension of its palatal-tooth lamella all the way to (*vs.* stopping before) the apertural-lip edge. Differs from *G. a. rakotomalalai* subsp. nov. in its smaller initial whorl (diameter of first 1.5 whorls 1.075-1.100 mm vs. 1.150-1.168 mm).

HOLOTYPE. Station 417 (UF 274670, 1 ad): 13°06'S, 49°13'E: Madagascar: Andavakoera, N of Betsiaka, 230 m: dry deciduous forest. 30-Aug-95.

OTHER DRY PARATYPES. Stations 413 (UF 274672, 1 juv); 417 (UF 274674, 28 ad, 10 juv); 418 (UF 274673, 37 ad, 18 juv); 421 (UF 274675, 3 ad, 4 juv; UF 274671, 1 ad).

ALCOHOL PARATYPES. Stations 413 (UF 273657, 2 ad, 1 juv); 417 (UF 273660, 2 ad); 418 (UF 273656, 2 ad).

DESCRIPTION OF HOLOTYPE. Height 5.9 mm, diameter 2.8 mm (H/D 2.1), whorls 6.5 (whorls/ln height 3.68). Apical angle 95°, barreling 3.5%. Sutural depth 6.0%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 1.08 mm, embryonic sculpture smooth. Peristome height 2.1 mm, width 1.9 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.38 mm (0.17 peristome W). Apertural barriers consisting of a large parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a moderate columellar recessed baffle; and a strong baso-columellar lamella. Umbilicus a crevice.

VARIATION. See Table 4.

ETYMOLOGY. For the Andavakoera massif, north of Betsiaka.

Gulella ambrensis rakotomalalai subsp. nov.
Fig. 45

DIAGNOSIS. Known only from Analamera Reserve. Differs from *G. ambrensis s.s.* sp. nov., *G. a. andavakoerae* subsp. nov., and both other subspecies of *G. ambrensis* sp. nov. in its larger initial whorl (diameter of first 1.5 whorls 1.150-1.168 mm *vs.* 1.025-1.100 mm). Further differs from *G. ambrensis s.s.* sp. nov. in its strong (*vs.* weak) sutural crenulation, deciduous-forest (*vs.* rainforest) habitat, and extension of the palatal-tooth lamella all the way to (*vs.* stopping before) the apertural-lip edge. Further differs from *G. a. capdambri* subsp. nov. in its non-recessed (*vs.* often recessed) palatal tooth. Further differs from *G. a. orangea* subsp. nov. in its looser coiling (whorls/ln height 3.76-3.87 *vs.* 3.88-3.98) and in the extension of its palatal-tooth lamella all the way to (*vs.* stopping before) the apertural-lip edge.

HOLOTYPE. Station 208 (UF 274648, 1 ad): 12°44'S, 49°30'E: Madagascar: Analamera Reserve, 100 m: dry deciduous forest. 16-Jul-95.

DRY PARATYPES. Stations 204 (UF 274651, 1 juv); 206 (UF 274650, 1 ad, 1 juv); 208 (UF 274653, 2 ad); 210 (UF 274649, 2 ad, 1 juv); 213 (UF 274652, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 6.0 mm, diameter 2.5 mm (H/D 2.4), whorls 6.7 (whorls/ln height 3.76). Apical angle 95°, barreling 5.0%. Sutural depth 9.0%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.8, diameter of first 1.5 whorls 1.17 mm, embryonic sculpture smooth, with a trace of sutural notches. Peristome height 1.8 mm, width 1.8 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.26 mm (0.14 peristomeW). Apertural barriers consisting of a large parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a moderate columellar recessed baffle; and a strong baso-columellar lamella. Umbilicus a crevice.

VARIATION. See Table 4.

ETYMOLOGY. In honor of the late Max Felix Rakotomalala, assistant and friend.

Gulella ambrensis capdambri subsp. nov.
Fig. 46

DIAGNOSIS. Known only from Cap d'Ambre. Differs from *G. ambrensis s.s.* sp. nov. and all other subspecies of *G. ambrensis* sp. nov. in its often recessed (*vs.* non-recessed) palatal tooth. Further differs from *G. ambrensis s.s.* sp. nov. in its strong (*vs.* weak) sutural crenulation and deciduous-forest (*vs.* rainforest) habitat. Further differs from *G. a. andavakoerae* subsp. nov. in its palatal-tooth lamella stopping before (*vs.* extending all the way to) the apertural-lip edge. Further differs from *G. a. orangea* subsp. nov. in its larger initial whorl (diameter of first 1.5 whorls 1.058-1.100 mm *vs.* 1.025-1.038 mm). Further differs from *G. a. rakotomalalai* subsp. nov. in its smaller initial whorl (diameter of first 1.5 whorls 1.025-1.038 mm *vs.* 1.150-1.168 mm).

HOLOTYPE. Station 230 (UF 274688, 1 ad): 11°57'S, 49°16'E: Madagascar: Cap d'Ambre, near lighthouse, 20 m: dry deciduous forest. 24-Jul-95.

DRY PARATYPES. Stations 230 (UF 274691, 6 ad, 2 juv); 233 (UF 274692, 22 ad, 5 juv; AMS C203574, 1 ad; ANSP 403466, 1 ad; MNHN, 1 ad); 238 (UF 274690, 1 ad, 3 juv); 240 (UF 274689, 2 ad, 1 juv).

ALCOHOL PARATYPES. Station 230 (UF 275066, 2 ad).

DESCRIPTION OF HOLOTYPE. Height 6.8 mm, diameter 3.0 mm (H/D 2.3), whorls 7.4 (whorls/ln height 3.86).

Apical angle 115°, barreling 6.3%. Sutural depth 4.2%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.1, diameter of first 1.5 whorls 1.06 mm, embryonic sculpture smooth. Peristome height 2.3 mm, width 2.0 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.44 mm (0.22 peristome W). Apertural barriers consisting of a large parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a moderate, slightly nubbed columellar recessed baffle; and a strong baso-columellar lamella. Umbilicus a crevice.

VARIATION. See Tables 2, 4.

ETYMOLOGY. For Cap d'Ambre, NW of Diego Suarez.

Gulella ambrensis orangea subsp. nov.
Fig. 47

DIAGNOSIS. Known only from Forêt d'Orange, Cap Mine. Differs from *G. ambrensis s.s.* sp. nov. in its strong (*vs.* weak) sutural crenulation and its deciduous-forest (*vs.* rainforest) habitat. Differs from all other subspecies except *G. ambrensis s.s.* sp. nov. in its smaller initial whorl (diameter of first 1.5 whorls 1.025-1.038 mm *vs.* 1.058-1.168 mm). Further differs from *G. a. andavakoerae* subsp. nov. in its palatal-tooth lamella stopping before (*vs.* extending all the way to) the apertural-lip edge. Further differs from *G. a. capdambri* subsp. nov. in its non-recessed (*vs.* often recessed) palatal tooth. Further differs from *G. a. rakotomalalai* subsp. nov. in its tighter coiling (whorls/ln height 3.88-3.98 *vs.* 3.76-3.87) and in its palatal-tooth lamella stopping before (*vs.* extending all the way to) the apertural-lip edge.

HOLOTYPE. Station 225 (UF 274645, 1 ad): 12°14'S, 49°22'E: Madagascar: Forêt d'Orange, Baie des Dunes, Cap Mine, 6 m: scrub. 21-Jul-95.

DRY PARATYPES. Stations 224 (UF 274646, 8 ad, 4 juv; AMS C203603, 1 ad; ANSP 403467, 1 ad; MNHN, 1 ad); 225 (UF 274647, 1 ad).

ALCOHOL PARATYPES. Station 224 (UF 275067, 3 ad).

DESCRIPTION OF HOLOTYPE. Height 6.1 mm, diameter 2.4 mm (H/D 2.5), whorls 7.2 (whorls/ln height 3.97). Apical angle 90°, barreling 3.8%. Sutural depth 4.0%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.8, diameter of first 1.5 whorls 1.03 mm, embryonic sculpture smooth, with a trace of sutural notches. Peristome height 1.9 mm, width 1.8 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.34 mm (0.19 peristome W). Apertural barriers consisting of a large parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a moderate, nubbed columellar recessed baffle; and a strong baso-columellar lamella. Umbilicus a crevice.

VARIATION. See Tables 2, 4.

ETYMOLOGY. For Forêt d'Orange, Cap Mine, NE of Diego Suarez.

Gulella bemarahae sp. nov.
Fig. 49

DIAGNOSIS. Of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, and (c) general rib sculpture strong to moderate, in only two species does the rib sculpture continue undiminished from the upper to the lower suture: *G. bemarahae* sp. nov. and *G. nakamaroa* sp. nov. *G. bemarahae* sp. nov. differs from *G. nakamaroa* sp. nov. in its palatal tooth that is transverse and squarish (*vs.* a short spiral lamella that is triangular in apertural view); looser coiling (whorls/ln height about 3.65 *vs.* about 3.85); smaller initial whorl (diameter of first 1.5 whorls about 1.2 mm *vs.* about 1.3 mm); and columnar (*vs.* barreled) shell shape. *G. bemarahae* sp. nov. is more tightly coiled than either *G. josephinae* sp. nov. or *G. soulaiana* (whorls/ln height 3.65 *vs.* 3.2 and 3.4), and has a larger initial whorl than *G. rugosa* sp. nov. (diameter of first 1.5 whorls about 1.2 *vs.* about 1.0); it also has a strong baso-columellar lamella that is lacking or weak in those other species.

HOLOTYPE. Station 249 (UF 274798, 1 ad): 19°08'S, 44°50'E: Madagascar: Bemaraha Reserve, 100 m: tall riverine gallery forest. 16-Jun-95.

DRY PARATYPES. Stations 248 (UF 274799, 7 ad, 6 juv); 249 (UF 274800, 8 ad, 31 juv; AMS C203570, 5 ad, 10 juv; ANSP 403468, 1 ad; MNHN, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 9.4 mm, diameter 3.0 mm (H/D 3.1), whorls 8.2 (whorls/ln height 3.66). Apical angle 100°, barreling 3.3%. Sutural depth 5.0%, sutural crenulation moderate. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 1.7, diameter of first 1.5 whorls 1.20 mm, embryonic sculpture of extremely faint growth lines. Peristome height 2.5 mm, width 2.5 mm (0.8 shell D; peristome H/W 1.0); apertural lip width 0.45 mm (0.18 peristome W). Apertural barriers consisting of a large parietal tooth; a large, squarish palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; and a strong baso-columellar lamella. Umbilicus a crevice.

ETYMOLOGY. For Bemaraha Reserve.

Gulella nakamaroa sp. nov.
Fig. 50

DIAGNOSIS. *G. nakamaroa* sp. nov. is somewhat similar to the West African *G. sulcifera* (Morelet, 1883) but has much stronger apertural dentition and an angular instead of a rounded columellar insertion. *G. nakamaroa* sp. nov.

bears some resemblance to the West African *G. circumcisa* (Morelet, 1885) but has looser coiling, a much stronger palatal tooth, and an angular instead of a rounded columellar insertion. Of Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, and (c) general rib sculpture strong to moderate, in only two species does the rib sculpture continue undiminished from the upper to the lower suture: *G. nakamaroa* sp. nov. and *G. bemarahae* sp. nov. *G. nakamaroa* sp. nov. differs from *G. bemarahae* sp. nov. in its palatal tooth that is a short spiral lamella appearing triangular in apertural view (*vs.* transverse and squarish); tighter coiling (whorls/ln height about 3.85 *vs.* about 3.65); larger initial whorl (diameter of first 1.5 whorls about 1.3 mm *vs.* about 1.2 mm); and barreled (*vs.* columnar) shell shape. *G. nakamaroa* sp. nov. differs rather markedly from all other two-toothed, ribbed, Madagascan species of *Gulella*.

HOLOTYPE. Station 805 (UF 274959, 1 ad): 13°01'S, 49°00'E: Madagascar: Ankarana Reserve, 50 m. 8-Oct-94.

DRY PARATYPES. Station 805 (UF 274960, 22 ad, 17 juv; AMS C203601, 22 ad, 17 juv; ANSP 403469, 1 ad; MNHN, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 8.7 mm, diameter 3.7 mm (H/D 2.4), whorls 8.3 (whorls/ln height 3.84). Apical angle 90°, barreling 6.8%. Sutural depth 5.4%, sutural crenulation moderate. In apertural view, penultimate and body whorls with strong rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 2.0, diameter of first 1.5 whorls 1.28 mm, embryonic sculpture of minute riblets. Peristome height 2.6 mm, width 2.5 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.55 mm (0.22 peristome W). Apertural barriers consisting of a large parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; and a moderate baso-columellar lamella. Umbilicus imperforate.

ETYMOLOGY. For the many (Malagasy "maro") specimens taken (Malagasy "naka") at the single known locality.

Gulella capmini sp. nov.
Figs. 48, 51

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, and (c) strong-to-moderate rib sculpture that diminishes conspicuously between the upper and lower sutures, *G. capmini* sp. nov. is unique both in having its columellar recessed baffle conspicuous, nubbed, and toothlike; and in having the palatal tooth recessed about as deeply as the recessed columellar baffle. *G. capmini* sp. nov. occurs sympatrically with *G. ambrensis orangea* subsp. nov., which is superficially similar but has smooth sculpture, looser coiling, and a larger initial whorl.

HOLOTYPE. Station 225 (UF 274815, 1 ad): 12°14'S, 49°22'E: Madagascar: Baie des Dunes, Cap Mine, 6 m: scrub. 21-Jul-95.

DRY PARATYPES. Stations 224 (UF 274817, 3 ad, 2 juv); 225 (UF 274816, 7 ad, 1 juv; AMS C203575, 1 ad; ANSP 403470, 1 ad; MNHN, 1 ad).

ALCOHOL PARATYPES. Station 224 (UF 275084, 3 ad)

DESCRIPTION OF HOLOTYPE. Height 4.8 mm, diameter 2.5 mm (H/D 1.9), whorls 6.8 (whorls/ln height 4.33). Apical angle 120°, barreling 0.0%. Sutural depth 3.7%, sutural crenulation moderate. In apertural view, penultimate and body whorls with moderate rib sculpture that diminishes completely between upper and lower sutures. Embryonic whorls 2.2, diameter of first 1.5 whorls 1.08 mm, embryonic sculpture smooth. Peristome height 1.5 mm, width 1.7 mm (0.7 shell D; peristome H/W 0.9); apertural lip width 0.25 mm (0.15 peristome W). Apertural barriers consisting of a moderate parietal tooth; a large, rounded palatal tooth (parietal-palatal embayment moderately wide); a moderate, rather shallowly recessed columellar recessed baffle; and a strong baso-columellar lamella. Umbilicus a crevice.

VARIATION. See Tables 2, 3.

ETYMOLOGY. For Cap Mine, E of Diego Suarez.

Gulella marojejyae sp. nov.
Fig. 52

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, (c) strong-to-moderate rib sculpture that diminishes conspicuously between the upper and lower sutures, (d) columellar recessed baffle inconspicuous, broadly rounded, and not toothlike, and (e) palatal tooth much shallower than the recessed columellar baffle, *G. marojejyae* sp. nov. is unique in its large, loosely coiled shell (whorls/ln height about 3.3-3.4 *vs.* 4.1-4.6, diameter of first 1.5 whorls 1.0-1.1 mm *vs.* 0.8-0.9 mm). *G. marojejyae* sp. nov. is somewhat similar to *G. masoalae* sp. nov. in size, coiling, and apertural dentition, but is smaller in initial whorl (diameter of first 1.5 whorls 1.0-1.1 mm *vs.* 1.25-1.35 mm) and has half-ribbed (*vs.* smooth) sculpture. *G. marojejyae* sp. nov. bears some resemblance to *G. michellae* sp. nov., with which it is sometimes sympatric but from which it differs in its diminished (*vs.* undiminished) ribbing, its absence (*vs.* presence) of a baso-columellar tooth, and its much looser coiling (whorls/ln height 3.3 vs. 4.0).

HOLOTYPE. Station 649 (UF 274920, 1 ad): 14°29'S, 49°34'E: Madagascar: W Marojejy Reserve, 700 m: rainforest. 28-Sep-95.

DRY PARATYPES. Stations 612 (UF 274922, 1 juv); 645 (UF 274927, 2 ad); 648 (UF 274921, 1 ad); 649 (UF 274926, 2 ad, 1 juv; AMS C203597, 1 ad; ANSP 403471, 1 ad; MNHN, 1 ad); 650 (UF 274923, 1 ad); 679 (UF

274925, 1 ad); 680 (UF 274924, 1 ad).

ALCOHOL PARATYPES. Stations 627 (UF 275128, 1 ad); 645 (UF 275127, 1 juv); 649 (UF 275126, 1 ad); 650 (UF 275125, 2 juv).

DESCRIPTION OF HOLOTYPE. Height 7.0 mm, diameter 3.2 mm (H/D 2.2), whorls 6.5 (whorls/ln height 3.34). Apical angle 85°, barreling 0.0%. Sutural depth 4.9%, sutural crenulation strong. In apertural view, penultimate and body whorls with moderate rib sculpture that diminishes completely between upper and lower sutures. Embryonic whorls 2.1, diameter of first 1.5 whorls 1.16 mm, embryonic sculpture smooth, with faint traces of minute riblets. Peristome height 2.4 mm, width 2.2 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.41 mm (0.19 peristome W). Apertural barriers consisting of a moderate parietal tooth; a large, broad, rounded, evenly buttressed palatal tooth (parietal-palatal embayment fairly narrow); a small columellar recessed baffle; and a strong baso-columellar lamella. Umbilicus an extremely minute, narrow crevice.

ETYMOLOGY. For Marojejy Reserve.

Gulella griffithsi sp. nov.
Fig. 53

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, (c) strong-to-moderate rib sculpture that diminishes conspicuously between the upper and lower sutures, (d) columellar recessed baffle inconspicuous, broadly rounded, and not toothlike, and (e) palatal tooth much shallower than the recessed columellar baffle, only two species have a small and tightly coiled shell (whorls/ln height about 4.1-4.6, diameter of first 1.5 whorls 0.8-0.9 mm): *G. griffithsi* sp. nov. and *G. tsara* sp. nov. *G. griffithsi* sp. nov. differs from *G. tsara* sp. nov. in its much looser coiling (whorls/ln height about 4.1-4.2 *vs.* 4.5-4.6), its large (*vs.* moderate) parietal tooth, and its deciduous-forest (*vs.* rainforest) habitat.

HOLOTYPE. Station 247 (UF 274834, 1 ad, 1 juv): 19°08'S, 44°52'E: Madagascar: S Bemaraha Reserve, 100 m: lush tall riverine gallery forest. 15-Jun-95.

DRY PARATYPES. Stations 247 (UF 274835, 1 ad; AMS C203580, 1 ad; ANSP 403472, 1 ad; MNHN, 1 ad); 489 (UF 274836, 1 ad, 1 juv; AMS C203581, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 4.4 mm, diameter 1.9 mm (H/D 2.4), whorls 6.3 (whorls/ln height 4.23). Apical angle 85°, barreling 0.0%. Sutural depth 6.0%, sutural crenulation strong. In apertural view, penultimate and body whorls with moderate rib sculpture that diminishes completely between upper and lower sutures. Embryonic whorls 1.8, diameter of first 1.5 whorls 0.84 mm, embryonic sculpture smooth. Peristome height 1.4 mm, width 1.5 mm (0.8 shell D; peristome H/W 1.0); apertural lip width 0.22 mm (0.15 peristome W). Apertural barriers consisting of a large parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; and a moderate baso-columellar lamella. Umbilicus a crevice.

ETYMOLOGY. For Owen Griffiths, the collector.

Gulella tsara sp. nov.
Fig. 54

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition restricted to a parietal tooth and a palatal tooth, (b) baso-columellar lamella strong to moderate, (c) strong-to-moderate rib sculpture that diminishes conspicuously between the upper and lower sutures, (d) columellar recessed baffle inconspicuous, broadly rounded, and not toothlike, and (e) palatal tooth much shallower than the recessed columellar baffle, only two species have a small and tightly coiled shell (whorls/ln height about 4.1-4.6, diameter of first 1.5 whorls 0.8-0.9 mm): *G. tsara* sp. nov. and *G. griffithsi* sp. nov. *G. tsara* sp. nov. differs from *G. griffithsi* sp. nov. in its much tighter coiling (whorls/ln height about 4.5-4.6 *vs.* 4.1-4.2), its moderate (*vs.* large) parietal tooth, and its rainforest (*vs.* deciduous-forest) habitat.

HOLOTYPE. Station 513 (UF 275000, 1 ad): 13°59'S, 48°47'E: Madagascar: Tsaratanana Reserve, 1525 m: rainforest. 14-Jun-95.

DRY PARATYPES. Stations 505 (AMS C203614, 1 ad); 513 (UF 275003, 1 juv); 514 (UF 275001, 1 juv); 527 (UF 275002, 1 ad, 1 juv); 535 (ANSP 403473, 1 ad; MNHN, 1 ad).

ALCOHOL PARATYPE. Station 95 (UF 275141, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 3.8 mm, diameter 1.9 mm (H/D 2.0), whorls 6.1 (whorls/ln height 4.55). Apical angle 85°, barreling 1.1%. Sutural depth 4.4%, sutural crenulation strong. In apertural view, penultimate and body whorls with moderate rib sculpture that diminishes completely between upper and lower sutures. Embryonic whorls 1.8, diameter of first 1.5 whorls 0.88 mm, embryonic sculpture smooth, with a trace of minute riblets. Peristome height 1.2 mm, width 1.3 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.20 mm (0.16 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; and a moderate baso-columellar lamella. Umbilicus a small crevice.

ETYMOLOGY. Both for its resemblance to a smaller version of *Gulella tsaratananae* sp. nov. and for its pleasing (Malagasy "tsara") appearance.

Gulella microstriata sp. nov.
Fig. 55

DIAGNOSIS. Among Madagascan *Gulella* having apertural dentition of parietal and palatal teeth and at least one other tooth, *G. microstriata* sp. nov. is unique in its

extremely dense rib sculpture.

HOLOTYPE. Station 816 (UF 274937, 1 ad): 12°55'S, 49°03'E: Madagascar: Ankarana Reserve, 100 m. 12-Oct-94.

DRY PARATYPE. Station 816 (UF 274938, 1 juv).

DESCRIPTION OF HOLOTYPE. Height 6.2 mm, diameter 2.7 mm (H/D 2.3), whorls 8.0 (whorls/ln height 4.38). Apical angle 75°, barreling 7.0%. Sutural depth 3.4%, sutural crenulation none. In apertural view, penultimate and body whorls with moderate and extremely dense rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 1.7, diameter of first 1.5 whorls 1.24 mm, embryonic sculpture of minute riblets. Peristome height 1.7 mm, width 1.7 mm (0.6 shell D; peristome H/W 1.0); apertural lip width 0.38 mm (0.22 peristome W). Apertural barriers consisting of a large parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; a strong baso-columellar lamella; and a very low, broadly rounded baso-columellar tooth. Umbilicus a crevice.

ETYMOLOGY. For the sculpture of small (English "micro-") ridges (Latin "striata").

Gulella kelibea sp. nov.
Fig. 56

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition of parietal and palatal teeth and at least one other tooth, and (b) general rib sculpture weak to none, *G. kelibea* sp. nov. is unique in both its extremely tight coiling (whorls/ln height about 5.4 *vs.* 3.6-5.0) and its lack of evident sutural crenulation.

HOLOTYPE. Station 426 (UF 274863, 1 ad): 23°00'S, 47°44'E: Madagascar: Manombo Reserve, 50 m: rainforest. 23-Jul-95.

DRY PARATYPES. Stations 423 (UF 274871, 1 ad, 3 juv); 424 (UF 274866, 1 ad, 5 juv); 425 (UF 274867, 7 ad, 1 juv); 426 (UF 274868, 3 ad, 1 juv); 427 (UF 274873, 3 ad); 428 (UF 274876, 6 ad); 429 (UF 274875, 1 ad); 430 (UF 274872, 3 ad, 1 juv); 432 (UF 274870, 5 ad); 433 (UF 274865, 1 ad); 434 (UF 274874, 1 ad); 435 (UF 274869, 7 ad, 6 juv; AMS C203586, 1 ad; ANSP 403474, 1 ad; MNHN, 1 ad); 1351 (UF 274864, 1 ad).

ALCOHOL PARATYPES. Stations 427 (UF 275103, 2 ad, 1 juv); 428 (UF 2751052 ad); 429 (UF 275102, 3 ad); 430 (UF 275101, 3 ad); 431 (UF 275100, 11 ad, 4 juv); 432 (UF 275099, 12 ad); 433 (UF 275106, 1 ad, 1 juv); 435 (UF 275104, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 2.8 mm, diameter 1.4 mm (H/D 2.0), whorls 5.5 (whorls/ln height 5.43). Apical angle 95°, barreling -0.9%. Sutural depth 5.3%, sutural crenulation none. In apertural view, penultimate and body whorls with weak rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 1.9, diameter of first 1.5 whorls 0.68 mm, embryonic sculpture smooth, with faint traces of growth lines. Peristome height 0.9 mm, width 1.0 mm (0.7 shell D; peristome H/W 0.9); apertural lip width 0.18 mm (0.18 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, peg-rounded palatal tooth (parietal-palatal embayment moderately wide); a small, nubbed columellar recessed baffle; and a moderate, rounded peg-shaped mid-columellar tooth. Umbilicus a minute well.

ETYMOLOGY. For its very (Malagasy "be") small (Malagasy "kely") size, with some word play in Malagasy ("big little").

Gulella bicolor (Hutton, 1834)
Fischer-Piette *et al.* (1994): fig. 50 (specimen)

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition of parietal and palatal teeth and at least one other tooth, and (b) general rib sculpture weak to none, (c) shell height 3.5 mm or greater, and (d) sutural crenulation moderate to strong, *G. bicolor* is unique in having a shell shape steeply pyramidal (*vs.* barreled to columnar), whorls/ln height about 3.6 (*vs.* about 3.7-5.0), and habitat restricted to gardens and settlements.

DESCRIPTION (based on illustration in Fischer-Piette *et al.*, 1994). Height 7.0 mm, diameter 2.0 mm (H/D 3.4), whorls 7.0 (whorls/ln height 3.60). Apical angle 65°, barreling -13.0%. Sutural depth 3.8%, sutural crenulation strong. In apertural view, penultimate and body whorls with strong rib sculpture that diminishes completely, not far below the upper suture. Peristome height 1.9 mm, width 1.8 mm (0.9 shell D; peristome H/W 1.0); apertural lip width 0.40 mm (0.20 peristome W). Apertural barriers consisting of a moderate parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment moderately wide); a large columellar recessed baffle; a moderate baso-columellar lamella; and a large baso-columellar tooth. Umbilicus a crevice.

Gulella analamerae sp. nov.
Fig. 57

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition of parietal and palatal teeth and at least one other tooth and (b) general rib sculpture weak to none, two species are distinguished by their large size due to very loose coiling (whorls/ln height about 3.7-3.8): *G. analamerae* sp. nov. and *G. vohimarae* sp. nov. *G. analamerae* sp. nov. differs from *G. vohimarae* sp. nov. in (a) its narrow (*vs.* broad) baso-columellar tooth, (b) its often present (*vs.* never present) upper-columellar tooth, (c) its tighter coiling (whorls/ln height about 3.8 *vs.* about 3.7), and (d) its smaller initial whorl (diameter of first 1.5 whorls about 1.0-1.1 mm *vs.* about 1.2 mm).

HOLOTYPE. Station 202 (UF 274676, 1 ad): 12°44'S, 49°30'E: Madagascar: Analamera Reserve, 310 m: dry deciduous forest. 16-Jul-95.

DRY PARATYPES. Stations 199 (UF 274681, 1 juv); 201 (UF 274684, 30 ad, 11 juv; AMS C203565, 1 ad; ANSP 403475, 1 ad; MNHN, 1 ad); 202 (UF 274678, 1 ad); 203 (UF 274683, 2 ad); 204 (16 ad, 9 juv, speci-

mens lost); 206 (UF 274686, 21 ad, 11 juv); 207 (UF 274682, 1 ad); 208 (UF 274679, 1 juv); 210 (UF 274677, 3 juv); 212 (UF 274685, 4 ad); 213 (UF 274687, 14 ad, 6 juv); 214 (UF 274680, 1 ad, 3 juv).

ALCOHOL PARATYPES. Station 203 (UF 273641, 2 ad).

DESCRIPTION OF HOLOTYPE. Height 9.8 mm, diameter 4.1 mm (H/D 2.4), whorls 8.7 (whorls/ln height 3.81). Apical angle 135°, barreling 7.3%. Sutural depth 4.4%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 1.06 mm, embryonic sculpture smooth. Peristome height 2.8 mm, width 3.0 mm (0.7 shell D; peristome H/W 0.9); apertural lip width 0.70 mm (0.23 peristome W). Apertural barriers consisting of a large parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment narrow); a moderate columellar recessed baffle; a strong baso-columellar lamella; a moderate, peg-like baso-columellar tooth; and a low, very broad mid-columellar tooth. Umbilicus a narrow crevice.

ETYMOLOGY. For Analamera Reserve.

Gulella vohimarae sp. nov.
Fig. 58

DIAGNOSIS. Among Madagascan *Gulella* having (a) apertural dentition of parietal and palatal teeth and at least one other tooth and (b) general rib sculpture weak to none, two species are distinguished by their large size due to very loose coiling (whorls/ln height about 3.7-3.8): *G. vohimarae* sp. nov. and *G. analamerae* sp. nov. *G. vohimarae* sp. nov. differs from *G. analamerae* sp. nov. in (a) its broad (*vs.* narrow) baso-columellar tooth, (b) its absent (*vs.* often present) upper-columellar tooth, (c) its looser coiling (whorls/ln height about 3.7 *vs.* about 3.8), and (d) its larger initial whorl (diameter of first 1.5 whorls about 1.2 mm *vs.* about 1.0-1.1 mm).

HOLOTYPE. Station 256 (UF 275053, 1 ad): 13°35'S, 49°59'E: Madagascar: S of Vohimar, 90 m: viny rainforest. 2-Sep-95.

DRY PARATYPES. Stations 256 (UF 275054, 6 ad, 4 juv; AMS C203622, 1 ad; ANSP 403476, 1 ad; MNHN, 1 ad); 257 (UF 275055, 3 ad).

ALCOHOL PARATYPES. Stations 256 (UF 275167, 1 ad); 257 (UF 275166, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 8.1 mm, diameter 3.1 mm (H/D 2.6), whorls 7.7 (whorls/ln height 3.68). Apical angle 95°, barreling 4.8%. Sutural depth 6.2%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.5, diameter of first 1.5 whorls 1.23 mm, embryonic sculpture of very faint growth lines. Peristome height 2.3 mm, width 2.2 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.50 mm (0.23 peristome W). Apertural barriers consisting of a large parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment narrow); a large columellar recessed baffle; a strong, recessed baso-columellar lamella; and a large, recessed, broadly rounded baso-columellar tooth that is high in position. Umbilicus imperforate.

ETYMOLOGY. For the city of Vohimar, near the type locality.

Gulella nosybei sp. nov.
Figs. 61, 102

DIAGNOSIS. *G. nosybei* sp. nov. is somewhat similar to the Comoran *G. cryptophora* (Morelet, 1881) but has very much looser coiling. *G. nosybei* sp. nov. is unique among Madagascan *Gulella* in its combination of (a) smooth sculpture; (b) tridentate aperture consisting of parietal, palatal, and mid-columellar teeth and small and inconspicuous recessed columellar baffle; and (c) stout and loosely coiled (whorls/ln height about 4.3, diameter of first 1.5 whorls about 0.9) shell with convex-edged to only slightly concave-edged outer peristome. *G. tendronia* sp. nov. is somewhat similar but much more tightly coiled, with a large columellar recessed baffle and a strongly concave-edged outer peristome. *G. kelibea* sp. nov. is similarly shaped but very much smaller and more tightly coiled, and with a conspicuously nubbed columellar recessed baffle.

HOLOTYPE. Station 118 (UF 274961, 1 ad): 13°25'S, 48°18'E: Madagascar: Lokobe Reserve, Nosy Be, 60 m: rainforest. 25-Jun-95.

FIGURED PARATYPE. Station 546 (UF 274962, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 4.2 mm, diameter 2.0 mm (H/D 2.1), whorls 6.2 (whorls/ln height 4.29). Apical angle 85°, barreling 1.0%. Sutural depth 5.3%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.9, diameter of first 1.5 whorls 0.89 mm, embryonic sculpture smooth. Peristome height 1.2 mm, width 1.2 mm (0.6 shell D; peristome H/W 1.0); apertural lip width 0.15 mm (0.13 peristome W). Apertural barriers consisting of a large parietal tooth; a large, oblique-butte-shaped palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; and a large, rounded-triangular mid-columellar tooth. Umbilicus imperforate, apparently.

ETYMOLOGY. For the island of Nosy Be.

Gulella tendronia sp. nov.
Fig. 59

DIAGNOSIS. Only two species of Madagascan *Gulella* have a combination of (a) smooth sculpture; (b) apertural dentition that includes parietal and palatal teeth and a low-positioned mid-columellar tooth; and (c) outer edge of peristome conspicuously concave: *G. tendronia* sp. nov. and *G. celestinae* sp. nov. *G. tendronia* sp. nov. differs from *G. celestinae* sp. nov. in its absence (*vs.* presence) of an upper-columellar tooth and its undivided (*vs.* bifid) parietal and

palatal teeth. *G. tendronia* sp. nov. differs from *G. nosybei* sp. nov. in its much tighter coiling, moderate (*vs.* small and inconspicuous) columellar recessed baffle, and strongly concave-edged outer peristome.

HOLOTYPE. Station 201 (UF 274999, 1 ad): 12°44'S, 49°30'E: Madagascar: Analamera Reserve, 315 m: dry deciduous forest. 15-Jul-95.

DRY PARATYPE. Station 201 (AMS C203613, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 3.7 mm, diameter 1.5 mm (H/D 2.5), whorls 6.2 (whorls/ln height 4.70). Apical angle 90°, barreling 2.6%. Sutural depth 5.3%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.78 mm, embryonic sculpture smooth, apparently. Peristome height 1.2 mm, width 1.1 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.13 mm (0.12 peristome W). Apertural barriers consisting of a large parietal tooth; a large, oblique-butte-shaped palatal tooth (parietal-palatal embayment moderately wide); a moderate columellar recessed baffle; and a large, rounded-triangular mid-columellar tooth that is low in position. Umbilicus a small crevice.

ETYMOLOGY. For its type locality, a summit (Malagasy "tendrony") within Analamera Reserve.

Gulella celestinae sp. nov.
Fig. 60

DIAGNOSIS. Only two species of Madagascan *Gulella* have a combination of (a) smooth sculpture; (b) apertural dentition that includes parietal and palatal teeth and a low-positioned mid-columellar tooth; and (c) outer edge of peristome conspicuously concave: *G. celestinae* sp. nov. and *G. tendronia* sp. nov. *G. celestinae* sp. nov. differs from *G. tendronia* sp. nov. in its presence (*vs.* absence) of an upper-columellar tooth and its bifid (*vs.* undivided) parietal and palatal teeth. *G. celestinae* sp. nov. is sympatric with the morphologically similar *G. vakinifia* sp. nov., from which it differs in its smooth (*vs.* strongly ribbed) sculpture and its presence (*vs.* absence) of an upper-columellar tooth.

HOLOTYPE. Station 74 (UF 274818, 1 ad): 16°23'S, 45°20'E: Madagascar: Namoroka Reserve, 100 m: dry deciduous forest. 28-May-95.

DRY PARATYPES. Station 74 (UF 274819, 22 ad, 7 juv).

DESCRIPTION OF HOLOTYPE. Height 4.4 mm, diameter 1.9 mm (H/D 2.4), whorls 7.2 (whorls/ln height 4.80). Apical angle 95°, barreling 5.2%. Sutural depth 10.2%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.84 mm, embryonic sculpture smooth. Peristome height 1.3 mm, width 1.2 mm (0.6 shell D; peristome H/W 1.1); apertural lip width 0.26 mm (0.21 peristome W). Apertural barriers consisting of a large, slightly bifid parietal tooth; a large, bifid palatal tooth (parietal-palatal embayment rather narrow); a moderate columellar recessed baffle; a large, peg-like mid-columellar tooth; and a moderate upper-columellar tooth. Umbilicus a minute crevice.

VARIATION. See Table 2.

ETYMOLOGY. For Celestine Ruth Emberton, daughter of the author, who was near the type locality when she was five months old.

Gulella bemoka sp. nov.
Fig. 62

DIAGNOSIS. Only two species of Madagascan *Gulella* have a combination of (a) smooth sculpture; (b) apertural dentition consisting of parietal, palatal teeth, and baso-columellar teeth; and (c) palatal and columellar sides of the peristome straight, parallel, and slanted conspicuously toward the umbilicus: *G. bemoka* sp. nov. and *G. vavakelia* sp. nov. *G. bemoka* sp. nov. differs from *G. vavakelia* sp. nov. in having its palatal tooth notched to receive the parietal tooth and inwardly slanting downward.

HOLOTYPE. Station 241 (UF 274801, 1 ad): 12°00'S, 49°17'E: Madagascar: Cap d'Ambre, near Ambatojanahary, 15 m: dry deciduous forest. 25-Jul-95.

DESCRIPTION OF HOLOTYPE. Height 5.6 mm, diameter 2.1 mm (H/D 2.6), whorls 7.7 (whorls/ln height 4.49). Apical angle 105°, barreling 5.9%. Sutural depth 5.8%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.1, diameter of first 1.5 whorls 0.88 mm, embryonic sculpture smooth. Peristome height 1.7 mm, width 1.5 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.31 mm (0.21 peristome W). Apertural barriers consisting of a moderate parietal tooth; a very large palatal tooth, notched opposite the parietal tooth (parietal-palatal embayment narrow, nearly enclosed); a large columellar recessed baffle; a moderate baso-columellar lamella; and a moderate baso-columellar tooth. Umbilicus imperforate.

ETYMOLOGY. Both for the many mosquitoes at the type locality (Malagasy "be" = many, "moka" = mosquitoes) and for the villagers of Bemoka who helped collect there.

Gulella vavakelia sp. nov.
Fig. 63

DIAGNOSIS. Only two species of Madagascan *Gulella* have a combination of (a) smooth sculpture; (b) apertural dentition consisting of parietal, palatal teeth, and baso-columellar teeth; and (c) palatal and columellar sides of the peristome straight, parallel, and slanted conspicuously toward the umbilicus: *G. vavakelia* sp. nov. and *G. bemoka* sp. nov. *G. vavakelia* sp. nov. differs from *G. bemoka* sp. nov. in its unnotched palatal tooth that does not inwardly

slant downward.

HOLOTYPE. Station 199 (UF 275004, 1 ad): 12°43'S, 49°28'E: Madagascar: Analamera Reserve, 35 m: dry deciduous forest. 15-Jul-95.

DRY PARATYPES. Stations 199 (UF 275005, 16 ad, 5 juv; AMS C203621, 3 ad; ANSP 403477, 3 ad; MNHN, 3 ad); 201 (UF 275006, 7 ad); 208 (UF 275007, 1 ad).

ALCOHOL PARATYPES. Stations 199 (UF 275164, 3 ad) 201 (UF 275165, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 5.8 mm, diameter 2.1 mm (H/D 2.7), whorls 7.8 (whorls/ln height 4.43). Apical angle 90°, barreling 4.4%. Sutural depth 5.7%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.85 mm, embryonic sculpture smooth. Peristome height 1.5 mm, width 1.4 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.28 mm (0.20 peristome W). Apertural barriers consisting of a large parietal tooth; a very large, acutely triangular palatal tooth (parietal-palatal embayment fairly narrow, nearly enclosed); a large columellar recessed baffle; a strong, recessed baso-columellar lamella; and a moderate, recessed baso-columellar tooth that is high in position. Umbilicus a very tiny crevice.

ETYMOLOGY. For the small aperture (Malagasy "vava" = mouth, "kely" = small).

Gulella mitsikia sp. nov.
Fig. 64

DIAGNOSIS. Among Madagascan *Gulella* having (a) smooth sculpture; (b) apertural dentition consisting of parietal, palatal teeth, and baso-columellar teeth; and (c) palatal and columellar sides of the peristome curved, non-parallel, and not slanted conspicuously inward, *G. mitsikia* sp. nov. is unique in having (a) its baso-columellar tooth large and buttressed more strongly above than below, and (b) its palatal tooth slightly bifid.

HOLOTYPE. Station 579 (UF 274945, 1 ad): 12°58'S, 49°06'E: Madagascar: Ankarana Reserve, 100 m: dry deciduous forest. 25-Aug-95.

DRY PARATYPES. Stations 577 (UF 274947, 10 ad, 11 juv); 579 (UF 274948, 5 ad, 2 juv); 580 (UF 274946, 23 ad, 17 juv; AMS C203600, 3 ad; ANSP 403478, 3 ad; MNHN, 3 ad).

ALCOHOL PARATYPES. Stations 577 (UF 273652, 1 ad); 580 (UF 273653, 2 ad).

DESCRIPTION OF HOLOTYPE (apex broken during measurement). Height 3.6 mm, diameter 1.6 mm (H/D 2.2), whorls estimated at 6.2 (whorls/ln height 4.88). Apical angle 90°, barreling 3.8%. Sutural depth 2.7%, sutural crenulation moderate. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.9, diameter of first 1.5 whorls 0.83 mm, embryonic sculpture smooth. Peristome height 1.1 mm, width 1.0 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.12 mm (0.12 peristome W). Apertural barriers consisting of a large, very slightly bifid parietal tooth; a large, slightly notched palatal tooth (parietal-palatal embayment fairly wide); a moderate columellar recessed baffle; a strong baso-columellar lamella; and a large baso-columellar tooth. Umbilicus a narrow well.

ETYMOLOGY. "To smile" (Malagasy "mitsiky"), for the appearance of the small and toothy aperture.

Gulella bobaombiae sp. nov.
Figs. 65, 66, 67

DIAGNOSIS. Among Madagascan *Gulella* having (a) smooth sculpture; (b) apertural dentition consisting of parietal, palatal teeth, and baso-columellar teeth; and (c) baso-columellar tooth buttressed equally above and below, *G. bobaombiae* sp. nov. is unique in its small and tightly coiled shell (whorls/ln height 4.9-5.1, diameter of first 1.5 whorls 0.7-0.8 mm).

HOLOTYPE. Station 401 (UF 274803, 1 ad): 12°11'S, 49°13'E: Madagascar: Cap d'Ambre, la Butte Bobaomby, 205 m: dry deciduous-baobab forest. 24-Aug-95.

FIGURED PARATYPES. Stations 222 (UF 274804, 1 ad); 229 (UF 274805, 1 ad).

OTHER DRY PARATYPES. Stations 222 (UF 274807, 1 ad); 229 (UF 274808, 3 ad, 1 juv); 401 (UF 274806, 5 ad, 1 juv; AMS C203572, 1 ad; ANSP 403479, 1 ad; MNHN, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 4.2 mm, diameter 1.7 mm (H/D 2.5), whorls 7.1 (whorls/ln height 4.91). Apical angle 115°, barreling 3.6%. Sutural depth 5.7%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 2.2, diameter of first 1.5 whorls 0.74 mm, embryonic sculpture smooth, with a trace of growth lines. Peristome height 1.3 mm, width 1.2 mm (0.7 shell D; peristome H/W 1.0); apertural lip width 0.24 mm (0.19 peristome W). Apertural barriers consisting of a large parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment moderately wide); a moderate columellar recessed baffle; a moderate baso-columellar lamella; and a moderate, knob-like baso-columellar tooth. Umbilicus a minute crevice.

VARIATION. See Table 3.

ETYMOLOGY. For the Butte Bobaomby, sole known locality, and for Cap d'Ambre (Malagasy name Tanjona Bobaomby).

Gulella ambanikelia sp. nov.
Figs. 68, 103

DIAGNOSIS. Among Madagascan *Gulella* having (a) smooth penultimate-whorl sculpture; (b) apertural dentition consisting of parietal, palatal teeth, and baso-columellar teeth; (c) baso-columellar tooth buttressed equally above and below; (d) whorls/ln height 4.0-4.4; and (e) diameter of

first 1.5 whorls 0.9-1.0 mm, *G. ambanikelia* sp. nov is unique both in the ribbed sculpture of its upper whorls, and in the knobbed shape of its baso-columellar tooth.

HOLOTYPE. Station 805 (UF 274654, 1 ad): 13°01'S, 49°00'E: Madagascar: Ankarana Reserve, 50 m. 8-Oct-94.

FIGURED PARATYPE. Station 805 (UF 274655, 1 ad).

OTHER DRY PARATYPES. Stations 803 (UF 274656, 1 ad); 805 (UF 274657, 50 ad, 3 juv; AMS C203563, 1 ad; ANSP 403480, 1 ad; MNHN, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 5.6 mm, diameter 2.3 mm (H/D 2.5), whorls 7.5 (whorls/ln height 4.37). Apical angle 120°, barreling 4.2%. Sutural depth 4.2%, sutural crenulation strong. In apertural view, penultimate and body whorls smoothish, without rib sculpture. Embryonic whorls 1.9, diameter of first 1.5 whorls 0.88 mm, embryonic sculpture of extremely faint growth lines. Peristome height 1.4 mm, width 1.6 mm (0.7 shell D; peristome H/W 0.8); apertural lip width 0.36 mm (0.22 peristome W). Apertural barriers consisting of a large parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment narrow); a moderate columellar recessed baffle; a moderate baso-columellar lamella; and a moderate, recessed baso-columellar tooth. Umbilicus imperforate.

VARIATION. Fig. 103 shows a neoadult with only partially formed apertural barriers and lip.

ETYMOLOGY. For the small (Malagasy "kely") tooth on the basal area (Malagasy "ambany") of the aperture.

Gulella ambalaniranae sp. nov.
Figs. 71, 72, 73, 74

DIAGNOSIS. *G. ambalaniranae* sp. nov. is unique among Madagascan *Gulella* in its combination of (a) strong rib sculpture that diminishes completely above the lower suture, and (b) apertural dentition consisting of undivided parietal, palatal, and baso-columellar teeth.

HOLOTYPE. Station 267 (UF 276304, 1 ad): 13°50'S, 49°59'E: Madagascar: Ambalanirana Mountain, 315 m: rainforest. 5-Sep-95.

FIGURED PARATYPES. Station 712 (UF 274631, 3 ad).

OTHER DRY PARATYPES. Stations 258 (UF 274637, 2 ad, 2 juv); 259 (UF 274639, 1 ad); 260 (UF 274634, 1 juv); 261 (UF 274640, 5 ad, 1 juv); 262 (UF 274644, 13 ad, 7 juv); 263 (UF 274632, 1 juv); 264 (UF 274633, 1 ad); 265 (UF 274643, 5 ad, 1 juv); 266 (UF 274641, 2 ad); 267 (UF 274642, 6 ad, 7 juv); 711 (UF 274636, 1 ad); 712 (UF 274635, 85 ad, 19 juv; AMS C203562, 3 ad; ANSP 403481, 3 ad; MNHN, 3 ad); 714 (UF 274638, 2 ad).

ALCOHOL PARATYPES. Stations 258 (UF 273638, 2 ad); 260 (UF 273637, 1 ad); 261 (UF 273634, 1 ad); 262 (UF 273632, 11 ad, 2 juv); 265 (UF 273635, 3 ad, 1 juv); 266 (UF 273639, 1 ad); 267 (UF 273633, 8 ad); 270 (UF 273636, 2 juv); 712 (UF 273631, 86 ad, 7 juv); 714 (UF 273640, 3 ad).

DESCRIPTION OF HOLOTYPE. Height 9.8 mm, diameter 3.8 mm (H/D 2.6), whorls 8.8 (whorls/ln height 3.86). Apical angle 95°, barreling 7.9%. Sutural depth 6.3%, sutural crenulation strong. In apertural view, penultimate and body whorls with moderate rib sculpture that diminishes completely between upper and lower sutures. Embryonic whorls 2.2, diameter of first 1.5 whorls 1.13 mm, embryonic sculpture of very faint growth lines. Peristome height 2.9 mm, width 2.7 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.75 mm (0.28 peristome W). Apertural barriers consisting of a massive parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment narrow); a large columellar recessed baffle; and a moderate baso-columellar tooth. Umbilicus imperforate.

VARIATION. Baso-columellar tooth sometimes absent.

ETYMOLOGY. For Mount Ambalanirana, N of Sambava.

Gulella namorokae sp. nov.
Fig. 75

DIAGNOSIS. *G. namorokae* sp. nov. is unique among Madagascan *Gulella* in its combination of (a) strong rib sculpture that diminishes completely above the lower suture, and (b) apertural dentition consisting of undivided parietal and baso-columellar teeth, and a strongly bifid palatal tooth.

HOLOTYPE. Station 58 (UF 274952, 1 ad): 16°25'S, 45°23'E: Madagascar: Namoroka Reserve, 120 m: dry deciduous forest. 23-May-95.

DRY PARATYPES. Stations 58 (UF 274954, 7 ad, 1 juv); 61 (UF 274955, 11 ad, 6 juv; AMS C203602, 1 ad; ANSP 403482, 1 ad; MNHN, 1 ad); 64 (UF 274953, 1 ad); 69 (UF 274956, 2 ad); 70 (UF 274958, 6 ad); 74 (UF 274957, 3 juv).

ALCOHOL PARATYPES. Stations 61 (UF 275132, 1 ad); 63 (UF 275133, 2 juv).

DESCRIPTION OF HOLOTYPE. Height 4.0 mm, diameter 1.8 mm (H/D 2.3), whorls 6.8 (whorls/ln height 4.91). Apical angle 100°, barreling 8.0%. Sutural depth 6.7%, sutural crenulation strong. In apertural view, penultimate and body whorls with strong rib sculpture that diminishes completely between upper and lower sutures. Embryonic whorls 1.9, diameter of first 1.5 whorls 0.83 mm, embryonic sculpture smooth. Peristome height 1.2 mm, width 1.1 mm (0.6 shell D; peristome H/W 1.1); apertural lip width 0.20 mm (0.19 peristome W). Apertural barriers consisting of a large parietal tooth; a very large, conspicuously bifid palatal tooth (parietal-palatal embayment wide); a moderate columellar recessed baffle; and a moderate baso-columellar tooth that is fairly high in position. Umbilicus an extremely minute crevice.

ETYMOLOGY. For Namoroka Reserve.

Gulella nihomelia sp. nov.
Figs. 76, 77, 78

DIAGNOSIS. *G. nihomelia* sp. nov. is somewhat similar to the South African *G. polita* (Melvill and Ponsonby, 1893) but has a mid-columellar instead of an upper-columellar tooth, has its palatal tooth higher in position and more narrowly based, and has very much looser coiling. *G.*

mihomehia sp. nov. is unique among Madagascan *Gulella* in its combination of (a) strong rib sculpture that diminishes completely above the lower suture, and (b) apertural barriers consisting of notched and closely fitting parietal and palatal teeth (the latter massive), a large columellar recessed baffle, and massive and peg-shaped mid-columellar and baso-central teeth (the latter offset toward the columella and unrecessed to deeply recessed). In apertural dentition, *G. mihomehia* sp. nov. is most similar to *G. vakinifia* sp. nov., from which it differs in its much looser coiling (whorls/ln height about 4.2 *vs.* 4.7-5.0) and its diminished (*vs.* undiminished) rib sculpture.

HOLOTYPE. Station 566 (UF 274949, 1 ad): 12°56'S, 49°07'E: Madagascar: Ankarana Reserve, 90 m: dry deciduous forest. 23-Aug-95.

FIGURED PARATYPES. Stations 568 (UF 274951, 1 ad); 580 (UF 274950, 1 ad).

OTHER DRY PARATYPES. Stations 566 (UF 274941, 7 ad); 568 (UF 274943, 1 ad); 580 (UF 274942, 4 ad); 803 (UF 274944, 93 ad, 71 juv; AMS C203599, 70 ad; ANSP 403483, 10 ad; MNHN, 10 ad); 807 (UF 274940, 2 ad); 815 (UF 274939, 1 ad, 3 juv).

DESCRIPTION OF HOLOTYPE. Height 6.0 mm, diameter 2.6 mm (H/D 2.3), whorls 7.5 (whorls/ln height 4.19). Apical angle 90°, barreling 2.4%. Sutural depth 1.3%, sutural crenulation moderate. In apertural view, penultimate and body whorls with strong rib sculpture that diminishes completely between upper and lower sutures. Embryonic whorls 2.0, diameter of first 1.5 whorls 1.05 mm, embryonic sculpture smooth, with a trace of growth lines. Peristome height 2.1 mm, width 1.7 mm (0.7 shell D; peristome H/W 1.2); apertural lip width 0.28 mm (0.17 peristome W). Apertural barriers consisting of notched and closely fitting parietal and palatal teeth (the latter massive); a large columellar recessed baffle; and massive, peg-shaped mid-columellar and baso-central teeth (the latter offset toward the columella and unrecessed [but deeply recessed in some paratypes]). Umbilicus a crevice.

ETYMOLOGY. "To laugh" (Malagasy "mihomehy"), for the appearance of the toothy aperture.

Gulella manomboae sp. nov.
Fig. 79

DIAGNOSIS. *G. manomboae* sp. nov. is somewhat similar to the East African *G. peculiaris* (E. A. Smith, 1890), but with much looser coiling and differently shaped apertural teeth. *G. manomboae* sp. nov. is unique among Madagascan *Gulella* for its embryonic sculpture of minute riblets and two subsutural spiral grooves. *G. manomboae* sp. nov. shares its undiminished rib sculpture and its apertural dentition of parietal, palatal, and baso-columellar teeth only with *G. michellae* sp. nov., from which it differs in its much smaller and more tightly coiled shell (whorls/ln height 4.6-4.7 *vs.* 4.0, diameter of first 1.5 whorls about 0.75 mm *vs.* about 1.15 mm).

HOLOTYPE. Station 433 (UF 274906, 1 ad): 23°00'S, 47°44'E: Madagascar: Manombo Reserve, 50 m: rainforest. 27-Feb-96.

DRY PARATYPES. Stations 423 (UF 274912, 4 ad); 424 (UF 274914, 6 ad); 425 (UF 274910, 2 juv); 426 (UF 274917, 2 ad); 427 (UF 274911, 4 ad); 428 (UF 274919, 3 ad, 1 juv; AMS C203596, 1 ad; ANSP 403486, 1 ad; MNHN, 1 ad); 429 (UF 274908, 4 ad, 1 juv); 430 (UF 274913, 4 ad, 1 juv); 431 (UF 274909, 3 ad); 432 (UF 274915, 3 ad, 1 juv); 433 (UF 274918, 1 juv); 435 (UF 274916, 1 juv); 1342 (ANSP 403484, 1 ad); 1347 (ANSP 403485, 1 ad, 1 juv).

ALCOHOL PARATYPES. Stations 427 (UF 275121, 4 ad); 428 (UF 275119, 2 ad, 1 juv); 429 (UF 275120, 8 ad); 430 (UF 275117, 3 ad); 431 (UF 275118, 7 ad); 432 (UF 275124, 4 ad); 433 (UF 275122, 4 ad, 1 juv); 434 (UF 275116, 1 ad); 435 (UF 275123, 3 ad); 1342 (ANSP A19194, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 3.6 mm, diameter 1.8 mm (H/D 2.0), whorls 6.0 (whorls/ln height 4.64). Apical angle 75°, barreling 2.2%. Sutural depth 3.6%, sutural crenulation moderate. In apertural view, penultimate and body whorls with strong rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 1.9, diameter of first 1.5 whorls 0.75 mm, embryonic sculpture of minute riblets and two subsutural spiral groves. Peristome height 1.2 mm, width 1.2 mm (0.7 shell D; peristome H/W 0.9); apertural lip width 0.22 mm (0.18 peristome W). Apertural barriers consisting of a moderate parietal tooth; a large, triangular palatal tooth curving upward to almost meet the parietal tooth (parietal-palatal embayment fairly wide, nearly enclosed); a large columellar recessed baffle; and a moderate, low, broad-triangular baso-columellar tooth. Umbilicus a very narrow well, opening obliquely.

ETYMOLOGY. For Manombo Reserve.

Gulella michellae sp. nov.
Fig. 80

DIAGNOSIS. *G. michellae* sp. nov. shares its undiminished rib sculpture and its apertural dentition of parietal, palatal, and baso-columellar teeth only with *G. manomboae* sp. nov., from which it differs in its much larger and more loosely coiled shell (whorls/ln height 4.0 *vs.* 4.6-4.7, diameter of first 1.5 whorls about 1.15 mm *vs.* about 0.75 mm). *G. michellae* sp. nov. bears some resemblance to *G. marojejyae* sp. nov., with which it is sometimes sympatric but from which it differs in its undiminished (*vs.* diminished) ribbing, its presence (*vs.* absence) of a baso-columellar tooth, and its much tighter coiling (whorls/ln height 4.0 *vs.* 3.3).

HOLOTYPE. Station 649 (UF 274821, 1 ad): 14°29'S, 49°34'E: Madagascar: W Marojejy Reserve, 700 m: rainforest. 28-Sep-95.

DRY PARATYPES. Stations 649 (UF 274823, 6 ad, 4 juv; AMS C203577, 1 ad; ANSP 403487, 1 ad; MNHN, 1 ad); 677 (UF 274822, 2 ad, 1 juv).

ALCOHOL PARATYPES. Station 649 (UF 273665, 4 ad).

DESCRIPTION OF HOLOTYPE. Height 7.0 mm, diameter 3.0 mm (H/D 2.3), whorls 7.7 (whorls/ln height 3.96). Apical angle 110°, barreling 9.3%. Sutural depth 6.1%, sutural crenulation moderate. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 2.1, diameter of first 1.5 whorls 1.14 mm, embryonic sculpture smooth. Peristome height 2.2 mm, width 1.9 mm (0.6 shell D; peristome H/W 1.1); apertural lip width 0.47 mm (0.24 peristome W). Apertural barriers consisting of a large parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment moderately wide); a moderate columellar recessed baffle; a strong baso-columellar lamella; and a low, broad-triangular baso-columellar tooth. Umbilicus a minute crevice.

ETYMOLOGY. For Michelle Kintana Emberton, daughter of the author.

Gulella mahagaga sp. nov.
Fig. 81

DIAGNOSIS. Among Madagascan *Gulella, G. mahagaga* sp. nov. is unique in its combination of (a) undiminished rib sculpture, (b) enormous columellar recessed baffle, and (c) apertural dentition consisting of parietal, palatal, mid-columellar, and baso-central teeth.

HOLOTYPE. Station 98 (UF 274895, 1 ad): 14°02'S, 48°47'E: Madagascar: Tsaratanana Reserve, 950 m: rainforest. 14-Jun-95.

DRY PARATYPES. Stations 98 (UF 274899, 6 ad, 2 juv; AMS C203594, 1 ad; ANSP 403488, 1 ad; MNHN, 1 ad); 103 (UF 274896, 1 ad); 110 (UF 274897, 1 ad); 112 (UF 274901, 6 ad, 1 juv); 114 (UF 274898, 1 ad, 2 juv); 502 (UF 274900, 1 juv).

ALCOHOL PARATYPES. Stations 98 (UF 273602, 1 ad); 112 (UF 273599, 5 ad); 114 (UF 273600, 1 ad); 504 (UF 273601, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 8.1 mm, diameter 3.5 mm (H/D 2.3), whorls 7.9 (whorls/ln height 3.78). Apical angle 85°, barreling 4.3%. Sutural depth 5.8%, sutural crenulation strong. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 2.2, diameter of first 1.5 whorls 1.34 mm, embryonic sculpture of minute riblets. Peristome height 2.6 mm, width 2.3 mm (0.7 shell D; peristome H/W 1.1); apertural lip width 0.40 mm (0.17 peristome W). Apertural barriers consisting of a moderate parietal tooth; a large, triangular palatal tooth (parietal-palatal embayment somewhat narrow); a massive columellar recessed baffle; a moderate, low, broad-triangular mid-columellar tooth; and a large, unrecessed baso-central tooth that is offset toward the columella. Umbilicus imperforate.

ETYMOLOGY. For the surprising (Malagasy "mahagaga") appearance of the apertural barriers.

Gulella hafa sp. nov.
Fig. 82

DIAGNOSIS. Among Madagascan *Gulella, G. hafa* sp. nov. is unique in its columellar dentition of basally merged upper-, mid-, and baso-columellar teeth.

HOLOTYPE. Station 593 (UF 274837, 1 ad): 14°26'S, 49°44'E: Madagascar: Marojejy Reserve, 1300 m: rainforest. 14-Sep-95.

DRY PARATYPES. Station 593 (AMS C203582, 1 ad; MNHN, 1 ad).

ALCOHOL PARATYPE. Station 593 (UF 275085, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 4.9 mm, diameter 2.5 mm (H/D 1.9), whorls 6.1 (whorls/ln height 3.85). Apical angle 80°, barreling 6.2%. Sutural depth 3.9%, sutural crenulation moderate. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 1.9, diameter of first 1.5 whorls 1.19 mm, embryonic sculpture of faint riblets. Peristome height 1.5 mm, width 1.4 mm (0.6 shell D; peristome H/W 1.0); apertural lip width 0.13 mm (0.09 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, peg-triangular palatal tooth (parietal-palatal embayment fairly wide); a small columellar recessed baffle; a moderate, wide baso-columellar tooth; a moderate, triangular mid-columellar tooth; and a moderate, wide upper-columellar tooth. All three columellar teeth are merged together at their bases. Umbilicus a very narrow well.

ETYMOLOGY. "Different" (Malagasy "hafa"), because it is so unlike other Madagascan species of *Gulella* in its columellar dentition.

Gulella benjamini Emberton and Pearce, 2000
Figs. 83, 84

DIAGNOSIS. Only three species of Madagascan *Gulella* have undiminished strong-to-moderate rib sculpture and apertural dentition restricted to parietal, palatal, and mid-columellar teeth: *G. benjamini, G. lubeti*, and *G. mahafinaratra* sp. nov. *G. benjamini* differs from the other two in its much smaller and more tightly coiled shell (whorls/ln height 4.8-5.4 vs. 4.0-4.1).

FIGURED SPECIMEN. Station 1419 (UF 274802, 1 ad).

DESCRIPTION OF HOLOTYPE (USNM 860808). Height 3.3 mm, diameter 1.8 mm (H/D 1.9), whorls 5.8 (whorls/ln height 4.81). Apical angle 100°, barreling 3.4%. Sutural depth 5.6%, sutural crenulation weak. In apertural view, penultimate and body whorls with moderate rib sculpture. Embryonic whorls 1.8, diameter of first 1.5 whorls 0.79 mm, embryonic sculpture of minute, faint riblets. Peristome height 1.1 mm, width 1.0 mm (0.6 shell D; peristome H/W 1.0); apertural lip width 0.18 mm (0.17 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, triangular palatal tooth (parietal-palatal embayment wide); a small columellar recessed

baffle; and a moderate mid-columellar tooth. Umbilicus a crevice.

VARIATION. See Tables 3, 4.

Gulella benjamini saintelucensis subsp. nov.
Fig. 85

DIAGNOSIS. Differs from *G. benjamini s.s.* in its much tighter coiling (whorls/ln height 5.4 *vs.* 4.8-4.9) and its coastal-rainforest (*vs.* montane-rainforest) habitat, that is now well separated from the parent species by uninhabitable, exotic savannah.

HOLOTYPE. Station 6 (UF 274990, 1 ad): 24°46'S, 47°09'E: Madagascar: Forêt Ste. Luce, 10 m: coastal rainforest. 29-Jan-95.

DRY PARATYPE. Station 6 (AMS C203571, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 3.0 mm, diameter 1.4 mm (H/D 2.1), whorls 5.9 (whorls/ln height 5.40). Apical angle 85°, barreling 2.6%. Sutural depth 6.4%, sutural crenulation weak. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.78 mm, embryonic sculpture smooth. Peristome height 0.9 mm, width 0.9 mm (0.6 shell D; peristome H/W 1.0); apertural lip width 0.18 mm (0.20 peristome W). Apertural barriers consisting of a moderate parietal tooth; a large, peg-triangular palatal tooth (parietal-palatal embayment wide); a small columellar recessed baffle; and a moderate, rounded mid-columellar tooth. Umbilicus a crevice.

ETYMOLOGY. For the coastal Forêt Sainte Luce.

Gulella lubeti Fischer-Piette, Blanc, Blanc and Salvat, 1994
Fischer-Piette *et al.* (1994): fig. 63 (holotype)

DIAGNOSIS. Only three species of Madagascan *Gulella* have undiminished strong-to-moderate rib sculpture and apertural dentition restricted to parietal, palatal, and mid-columellar teeth: *G. lubeti, G. mahafinaratra* sp. nov., and *G. benjamini*. Both *G. lubeti* and *G. mahafinaratra* sp. nov. differ from *G. benjamini* in their much larger and more loosely coiled shells (whorls/ln height 4.0-4.1 *vs.* 4.8-5.4). *G. lubeti* differs from *G. mahafinaratra* sp. nov. in that its columella is slanted conspicuously outward (*vs.* nearly vertical) and in its moderate (*vs.* very large) palatal tooth.

DESCRIPTION OF HOLOTYPE (based on illustration in Fischer-Piette *et al.*, 1994). Height 5.6 mm, diameter 2.6 mm (H/D 2.1), whorls 7.0 (whorls/ln height 4.06). Apical angle 85°, barreling 2.9%. Sutural depth 2.9%, sutural crenulation moderate. In apertural view, penultimate and body whorls with moderate rib sculpture that does not diminish between upper and lower sutures. Peristome height 1.5 mm, width 1.5 mm (0.6 shell D; peristome H/W 1.0); apertural lip width 0.20 mm (0.11 peristome W). Apertural barriers consisting of a moderate parietal tooth; a moderate, triangular palatal tooth (parietal-palatal embayment wide); a small columellar recessed baffle; a moderate baso-columellar lamella; and a moderate, triangular-rounded mid-columellar tooth.

Gulella mahafinaratra sp. nov.
Figs. 86, 87, 88

DIAGNOSIS. *G. mahafinaratra* sp. nov. is somewhat similar to the Comoran *G. brevicula* (Morelet, 1882) but has much looser coiling. Only three species of Madagascan *Gulella* have undiminished strong-to-moderate rib sculpture and apertural dentition restricted to parietal, palatal, and mid-columellar teeth: *G. mahafinaratra* sp. nov., *G. lubeti*, and *G. benjamini*. Both *G. mahafinaratra* sp. nov. and *G. lubeti* differ from *G. benjamini* in their much larger and more loosely coiled shells (whorls/ln height 4.0-4.1 *vs.* 4.8-5.4). *G. mahafinaratra* sp. nov. differs from *G. lubeti* in that its columella is nearly vertical (*vs.* slanted conspicuously outward) and its palatal tooth is very large (*vs.* moderate).

HOLOTYPE. Station 668 (UF 274886, 1 ad): 14°32'S, 49°42'E: Madagascar: E of Marojejy Reserve, 1500 m: cloudforest with bamboo. 5-Oct-95.

FIGURED PARATYPES. Stations 648 (UF 274888, 1 ad); 661 (UF 274887, 1 ad).

OTHER DRY PARATYPES. Stations 648 (UF 274890, 1 juv); 661 (UF 274891, 2 juv; MNHN, 1 ad); 666 (AMS C203593, 1 ad); 668 (UF 274889, 2 juv); 671 (UF 274894, 1 ad); 674 (UF 274893, 1 juv); 742 (UF 274892, 1 ad).

ALCOHOL PARATYPES. Stations 634 (UF 275108, 1 ad); 648 (UF 275114, 6 ad, 1 juv); 661 (UF 275112, 1 ad); 666 (UF 275110, 5 ad, 1 juv); 668 (UF 275109, 2 ad, 1 juv); 674 (UF 275113, 1 ad); 677 (UF 275115, 1 ad); 742 (UF 275111, 1 ad, 1 juv); 758 (UF 275107, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 7.2 mm, diameter 3.0 mm (H/D 2.4), whorls 8.0 (whorls/ln height 4.05). Apical angle 80°, barreling 5.2%. Sutural depth 5.2%, sutural crenulation weak. In apertural view, penultimate and body whorls with strong rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls estimated at 2.0, diameter of first 1.5 whorls 1.14 mm, embryonic sculpture smooth, apparently. Peristome height 2.0 mm, width 1.8 mm (0.6 shell D; peristome H/W 1.1); apertural lip width 0.44 mm (0.24 peristome W). Apertural barriers consisting of a moderate parietal tooth; a very large, triangular palatal tooth (parietal-palatal embayment fairly wide); a moderate columellar recessed baffle; and a moderate, rounded mid-columellar tooth. Umbilicus an extremely minute crevice.

ETYMOLOGY. For the beautiful (Malagasy "mahafinaratra") shell.

Gulella hafahafa sp. nov.
Figs. 89, 90, 91, 92

DIAGNOSIS. *G. hafahafa* sp. nov. is unique among

Madagascan *Gulella* both for its beaded embryonic sculpture and for its apertural dentition that includes upper-columellar, mid-columellar, and baso-central teeth.

HOLOTYPE. Station 349 (UF 274838, 1 ad): 16°19'S, 49°44'E: Madagascar: W of Sahasoa, S of Mananara, 480 m: hardwood rainforest. 18-Oct-95.

FIGURED PARATYPES. Stations 367 (UF 274839, 1 ad); 1540 (UF 274840, 1 juv); 1545 (UF 274841, 1 juv).

OTHER DRY PARATYPES. Stations 349 (UF 274844, 1 juv); 351 (UF 274845, 1 juv); 353 (UF 274843, 1 ad); 355 (UF 274842, 1 ad); 356 (UF 274847, 1 juv); 357 (UF 274846, 1 juv); 367 (UF 274848, 1 juv; AMS C203583, 1 ad; ANSP 403491, 1 ad; MNHN, 1 ad); 1529 (ANSP 403489, 1 juv); 1549 (ANSP 403490, 1 ad).

ALCOHOL PARATYPES. Stations 349 (UF 275091, 2 ad); 351 (UF 275088, 1 juv); 353 (UF 275089, 2 juv); 356 (UF 275087, 3 ad, 1 juv); 357 (UF 275090, 2 ad); 744 (UF 275086, 2 ad); 1529 (ANSP A19195, 1 juv); 1536 (ANSP A19196, 1 juv); 1540 (ANSP A19197); 1547 (ANSP A19198, 1 juv).

DESCRIPTION OF HOLOTYPE. Height 7.7 mm, diameter 3.4 mm (H/D 2.3), whorls 7.6 (whorls/ln height 3.73). Apical angle 80°, barreling 7.4%. Sutural depth 4.8%, sutural crenulation moderate. In apertural view, penultimate and body whorls with strong rib sculpture. Diameter of first 1.5 whorls 1.03 mm. Peristome height 2.8 mm, width 2.2 mm (0.7 shell D; peristome H/W 1.2); apertural lip width 0.75 mm (0.34 peristome W). Apertural barriers consisting of a massive parietal tooth; a massive, slightly bifid palatal tooth (parietal-palatal embayment narrow, nearly enclosed); a small columellar recessed baffle; a moderate, triangular mid-columellar tooth; a peg-like upper-columellar tooth; and a moderate baso-central tooth that is rather deeply recessed and offset toward the columella. Umbilicus a crevice.

DESCRIPTION OF EMBRYONIC SHELL OF PARATYPE UF 274839. Embryonic whorls 2.1, embryonic sculpture first smooth, then beaded (faint riblets interrupted by faint spiral striae).

ETYMOLOGY. For its unusual (Malagasy "hafahafa" = strange) apertural dentition.

VARIATION. See Table 3.

Gulella vatosoa sp. nov.
Fig. 93

DIAGNOSIS. Among Madagascan *Gulella, G. vatosoa* sp. nov. is unique in its strongly ribbed embryonic sculpture. Among species with undiminished strong rib sculpture and with apertural dentition restricted to parietal, palatal, and mid-columellar teeth, it is the only species in which the palatal and mid-columellar teeth point directly toward each other.

HOLOTYPE. Station 313 (UF 275043, 1 ad): 15°33'S, 49°59'E: Madagascar: W Masoala Peninsula, 305 m: hardwood rainforest. 28-Sep-95.

DRY PARATYPES. Stations 279 (UF 275044, 1 juv); 282 (UF 275048, 1 juv); 289 (UF 275045, 1 juv); 303 (UF 275046, 1 ad); 313 (UF 275051, 2 juv); 349 (UF 275052, 1 ad, 1 juv); 351 (UF 275049, 4 juv; ANSP 403492, 1 ad; MNHN, 1 ad); 353 (AMS C203620, 1 ad); 354 (UF 275050, 2 ad); 358 (UF 275047, 1 ad).

ALCOHOL PARATYPES. Stations 283 (UF 275154, 1 ad); 284 (UF 275161, 1 ad); 303 (UF 275157, 1 ad); 307 (UF 275160, 2 juv); 342 (UF 275159, 1 ad); 349 (UF 275155, 1 ad, 1 juv); 351 (UF 275156, 3 ad); 353 (UF 275158, 4 ad); 354 (UF 275162, 1 ad); 357 (UF 275163, 5 ad); 358 (UF 275153, 1 ad).

DESCRIPTION OF HOLOTYPE. Height 4.1 mm, diameter 2.1 mm (H/D 1.9), whorls 6.2 (whorls/ln height 4.41). Apical angle 80°, barreling 4.8%. Sutural depth 7.5%, sutural crenulation weak. In apertural view, penultimate and body whorls with very strong rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 1.9, diameter of first 1.5 whorls 0.80 mm, embryonic sculpture of strong riblets. Peristome height 1.4 mm, width 1.2 mm (0.6 shell D; peristome H/W 1.1); apertural lip width 0.28 mm (0.23 peristome W). Apertural barriers consisting of a large parietal tooth; a large, moderately bifid palatal tooth (parietal-palatal embayment moderately wide); a small columellar recessed baffle; and a large, peg-triangular mid-columellar tooth directly opposite the palatal tooth. Umbilicus a narrow well.

ETYMOLOGY. "Gem" (Malagasy "vatosoa"), for the pleasing appearance of the shell.

Gulella vakinifia sp. nov.
Figs. 94, 95, 96, 97

DIAGNOSIS. Among Madagascan species of *Gulella* with undiminished strong rib sculpture, *G. vakinifia* sp. nov. is unique in its apertural dentition of parietal, palatal, low-positioned mid-columellar, and recessed baso-central teeth. In apertural dentition, *G. vakinifia* sp. nov. is most similar to *G. mihomehia* sp. nov., from which it differs in its much tighter coiling (whorls/ln height about 4.7-5.0 *vs.* 4.2) and its undiminished (*vs.* diminished) rib sculpture. *G. vakinifia* sp. nov. is sometimes sympatric with the morphologically similar *G. celestinae* sp. nov., from which it differs in its ribbed (*vs.* smooth) sculpture and its absence (*vs.* presence) of an upper-columellar tooth.

HOLOTYPE. Station 254 (UF 275023, 1 ad): 19°02'S, 44°48'E: Madagascar: Bemaraha Reserve, 150 m: forest along limestone wall. 18-Jun-95.

FIGURED PARATYPES. Stations 62 (UF 275025, 1 ad); 254 (UF 275024, 1 ad); 490 (UF 275026, 1 ad).

OTHER DRY PARATYPES. Stations 61 (UF 275038, 1 ad, 1 juv); 62 (UF 275042, 3 ad, 1 juv); 64 (UF 275028, 4 ad); 65 (UF 275036, 3 ad); 68 (UF 275032, 4 ad); 74 (UF 275035, 30 ad, 1 juv; AMS C203619, 15 ad); 245 (UF 275027, 6 ad); 248 (UF 275041, 1 ad); 249 (UF 275034, 2 ad, 2 juv; AMS C203617, 8 ad, 2 juv); 252 (UF 275039, 1 ad); 254 (UF 275029, 2 ad; AMS C203618, 3 ad; ANSP 403493, 1 ad; MNHN, 1 ad); 489 (UF 275033, 4 ad); 490 (UF 275030, 7 ad, 5 juv); 494 (UF 275031, 6 ad).

ALCOHOL PARATYPES. Stations 64 (UF 275150, 2 ad); 65 (UF 275152, 1 ad); 490 (UF 275151, 2 ad).

DESCRIPTION OF HOLOTYPE. Height 3.5 mm, diameter 1.7 mm (H/D 2.1), whorls 6.3 (whorls/ln height 4.99) Apical angle 85°, barreling 5.7%. Sutural depth 4.8%, sutural crenulation strong. In apertural view, penultimate and body whorls with very strong rib sculpture Embryonic whorls 2.1, diameter of first 1.5 whorls 0.78 mm, embryonic sculpture smooth. Peristome height 1.6 mm, width 1.1 mm (0.6 shell D; peristome H/W 1.4); apertural lip width 0.30 mm (0.28 peristome W). Apertural barriers consisting of a massive, slightly notched parietal tooth; a massive, bifid palatal tooth (parietal-palatal embayment narrow); a moderate columellar recessed baffle; a moderate baso-columellar lamella; a moderate to large, rounded mid-columellar tooth; and a small, recessed baso-central tooth. Umbilicus a crevice.

VARIATION. See Tables 2, 3, 4.

ETYMOLOGY. For the split (Malagasy "vaky") palatal apertural tooth (Malagasy "nify").

Gulella orchida sp. nov.
Figs. 98, 99

DIAGNOSIS. Among Madagascan species of *Gulella* with undiminished strong rib sculpture, only two species have a palatal tooth that (a) is so massive it fills half the aperture and (b) has a notch into which the parietal tooth enters directly, and (c) that have a recessed baso-columellar tooth: *G. orchida* sp. nov. and *G. magnorchida* sp. nov. *G. orchida* sp. nov. differs from *G. magnorchida* sp. nov. in its presence (*vs.* absence) of an upper-columellar tooth, and in its tighter coiling (whorls/ln height 4.4-4.5 *vs.* 4.2-4.3).

HOLOTYPE. Station 218 (UF 274965, 1 ad): 12°23'S, 49°19'E: Madagascar: Montagne des Orchides, 385 m: dry deciduous forest. 20-Jul-95.

FIGURED PARATYPE. Station 221 (UF 274966, 1 ad).

OTHER DRY PARATYPES. Stations 215 (UF 274969, 6 ad, 1 juv); 217 (UF 274968, 18 ad, 2 juv); 218 (UF 274970, 17 ad, 8 juv); 221 (UF 274967, 30 ad, 6 juv; AMS C203604, 3 ad; ANSP 403494, 3 ad; MNHN, 3 ad).

ALCOHOL PARATYPES. Stations 215 (UF 275136, 3 ad); 218 (UF 275134, 3 ad); 221 (UF 275135, 5 ad).

DESCRIPTION OF HOLOTYPE. Height 5.8 mm, diameter 2.3 mm (H/D 2.5), whorls 7.5 (whorls/ln height 4.26). Apical angle 100°, barreling 5.4%. Sutural depth 5.4%, sutural crenulation strong. In apertural view, penultimate and body whorls with strong rib sculpture that diminishes little between upper and lower sutures. Embryonic whorls 2.0, diameter of first 1.5 whorls 0.89 mm, embryonic sculpture smooth. Peristome height 1.9 mm, width 1.5 mm (0.6 shell D; peristome H/W 1.3); apertural lip width 0.38 mm (0.25 peristome W). Apertural barriers consisting of a large parietal tooth, a massive, deeply notched palatal tooth, into which the parietal tooth enters (parietal-palatal embayment narrow, nearly enclosed); a large columellar recessed baffle; a strong baso-columellar lamella; a moderate baso-columellar tooth; and a large, low, rounded, mid-columellar tooth in a high position. Umbilicus imperforate.

ETYMOLOGY. Both for Montagne des Orchides and for the complex dentition reminiscent of orchid petals.

Gulella magnorchida sp. nov.
Fig. 100

DIAGNOSIS. Among Madagascan species of *Gulella* with undiminished strong rib sculpture, only two species have a palatal tooth that (a) is so massive it fills half the aperture and (b) has a notch into which the parietal tooth enters directly, and (c) that have a recessed baso-columellar tooth: *G. magnorchida* sp. nov. and *G. orchida* sp. nov. *G. magnorchida* sp. nov. differs from *G. orchida* sp. nov. in its absence (*vs.* presence) of an upper-columellar tooth, and in its looser coiling (whorls/ln height 4.2-4.3 *vs.* 4.4-4.5).

HOLOTYPE. Station 401 (UF 274881, 1 ad): 12°11'S, 49°13'E: Madagascar: Cap d'Ambre, la Butte Bobaomby, 205 m: dry deciduous-baobab forest. 24-Aug-95.

DRY PARATYPES. Stations 400 (UF 274883, 2 ad); 401 (UF 274884, 19 ad, 4 juv; AMS C203592, 1 ad; ANSP 403495, 1 ad; MNHN, 1 ad); 403 (UF 274882, 2 ad, 3 juv); 405 (UF 274885, 3 ad, 3 juv).

DESCRIPTION OF HOLOTYPE. Height 8.3 mm, diameter 2.8 mm (H/D 3.0), whorls 9.4 (whorls/ln height 4.43). Apical angle 105°, barreling 6.8%. Sutural depth 3.4%, sutural crenulation strong. In apertural view, penultimate and body whorls with strong rib sculpture that does not diminish between upper and lower sutures. Embryonic whorls 2.2, diameter of first 1.5 whorls 1.04 mm, embryonic sculpture smooth, with traces of miniscule riblets. Peristome height 2.3 mm, width 2.0 mm (0.7 shell D; peristome H/W 1.2); apertural lip width 0.47 mm (0.24 peristome W). Apertural barriers consisting of a large parietal tooth; a massive, broad palatal tooth notched to receive the parietal tooth (parietal-palatal embayment fairly narrow, nearly enclosed); a large columellar recessed baffle; a moderate baso-columellar lamella; and a moderate, rounded-peg-shaped baso-columellar tooth. Umbilicus imperforate.

ETYMOLOGY. For its resemblance to *Gulella orchida* sp. nov. and its diagnostically large (Latin "magn-") embryonic whorls.

ACKNOWLEDGEMENTS

Fieldwork, sorting, and identification were funded by the U.S. National Science Foundation (DEB 9201060/9596032); description was funded by Owen Griffiths. Permits were issued by the Madagascan government agencies DEF and ANGAP. Ranomafana National Park Project gave logistic support. Very many people assisted in the field and lab, but particular thanks go to Dr. Tim Pearce, Owen Griffiths, Jean Rakotoarison, and Roger Randalana. Dr. Fred Thompson helped with the literature. Two anonymous reviewers aided greatly.

LITERATURE CITED

Blanford, H. H. and H. H. Godwin-Austen. 1908. *Mollusca. Testacellidae and Zonitidae. The Fauna of British India, including Ceylon and Burma*, C. T. Bingham, ed. Series III, Volume 1: i-xxii, 1-311 plates 61-90. Taylor and Francis, London.

Bruggen, A. C. van. 1965. Descriptions of three new species of *Gulella* from southern Africa (Mollusca, Gastropoda Pulmonata: Streptaxidae). *Annals of the Natal Museum* 18:21-26.

Bruggen, A. C. van. 1966. Two new species of *Gulella* from southern Africa (Gastropoda, Pulmonata, Streptaxidae). *Archiv für Molluskenkunde* 95:69-73.

Bruggen, A. C. van. 1975a. Streptaxidae (Mollusca, Gastropoda: Pulmonata) from Aldabra Island, western Indian Ocean. *Bulletin of the British Museum of Natural History (Zoology)* 28:157-175.

Bruggen, A. C. van. 1975b. New taxa of Streptaxidae and Enidae (Mollusca, Gastropoda Pulmonata) from South Africa and Malawi. *Zoologische Mededelingen uttgegeven door het Rijksmuseum van Natuurlijke Historie te Leiden* 49:207-223.

Bruggen, A. C. van. 1980. Size clines and subspecies in the streptaxid genus *Gulella* Pfr. (Mollusca, Gastropoda Pulmonata) in southern Africa. *Zoologische Verhandelingen uttgegeven door het Rijksmuseum van Natuurlijke Historie te Leiden* 180:1-62.

Connolly, M. 1939. A monographic survey of South African non-marine Mollusca. *Annals of the South African Museum* 33:1-660, plates I-XIX.

Emberton, K. C. 1994. Thirty new species of Madagascan land snails. *Proceedings of the Academy of Natural Sciences of Philadelphia* 145:147-189.

Emberton, K. C. 1999. *Edentulina* of Madagascar (Pulmonata: Streptaxidae). *American Malacological Bulletin* 15:97-108.

Emberton, K. C. in press a. The genus *Boucardicus*, a Madagascan endemic (Caenogastropoda: Cyclophoracea: Alycaeidae). *Archiv für Molluskenkunde.*

Emberton, K. C. in press b. *Parvedentulina* and edentate *Gulella* of Madagascar (Pulmonata: Streptaxidae). *Archiv für Molluskenkunde.*

Emberton, K. C. and T. A. Pearce. 2000. Small, high-spired pulmonates from Mounts Mahermana, Ilapiry, and Vasiha, southeastern Madagascar, with description of a new genus, and with conservation statuses of 15 streptaxid species. *The Veliger* 43:126-153.

Emberton, K. C., T. A. Pearce and R. Randalana. 1996. Quantitatively sampling land-snail species richness in Madagascan rainforests. *Malacologia* 38:203-212.

Fischer-Piette, E., C. P. Blanc, F. Blanc and F. Salvat. 1993. Gastéropodes terrestres prosobranches. *Faune de Madagascar* 80:1-281.

Fischer-Piette, E., C. P. Blanc, F. Blanc and F. Salvat. 1994. Gastéropodes terrestres pulmonés. *Faune de Madagascar* 83:1-551.

Germain, L. 1923. *Mollusques terrestres et fluviatiles. Voyage de M. Guy Babault dans l'Afriques Orientale-Anglaise: Resultats scientifiques* pp. 1-149, plates I-IV. Paris.

Griffiths, O. 1996. Summary of the land snails of the Mascarene Islands with notes on their status. *Proceedings of the Royal Society of Arts and Sciences of Mauritius* 6:37-48.

Hanley, S. and W. Theobald. 1876. *Conchologica Indica*:i-xvii pp. 1-36, plates I-CLX. L. Reeve and Co., London.

Moellendorff, O. von and W. Kobelt. 1905. Die Raublungenschnecken (Agnatha). Erste Abtheilung: Rhytididae & Enneidae. *In: Systematisches Conchylien-Cabinet von Martini und Chemnitz*, H. C. Küster and W. Kobelt, eds., Ersten Bandes, Zwölfte Abtheilung (B.), Erste Hälfte:1-362, plates 1-41. Verlag von Bauer & Raspe (Emil Küster), Nürnberg.

Nordsieck, H. 1986. The system of the Stylommatophora (Gastropoda), with special regard to the systematic position of the Clausiliidae, II. Importance of the shell and distribution. *Archiv für Molluskenkunde* 117:93-116.

Pilsbry, H. A. 1919. A review of the land mollusks of the Belgian Congo chiefly based on the collections of the American Museum Congo Expedition, 1909-1915. *Bulletin of the American Museum of Natural History* 40:1-370, plates I-XXIII.

Richardson, C. L. 1988. Streptaxacea: catalog of species, Part 1, Streptaxidae. *Tryonia* 16:1-326.

Templeton, A. R. 1989. The meaning of species and speciation: A genetic perspective. *In: Speciation and its Consequences*, D. Otte and J. A. Endler, eds. pp. 3-27. Sinauer Associates, Sunderland, Massachusetts.

Verdcourt, B. 1961. The Gulellae (Moll., Streptaxidae) of the Usambara Mountains, N.E. Tanganyika. *Tanganyika Notes and Records* (1961):92-102, Figs. 1-29.

Verdcourt, B. 1962. Preliminary keys for the identification of the species of the genus Gulella Pfr. occurring in East Africa. *Musee Royal de l'Afrique Centrale, Tervuren, Belgique, Annales, Serie 8, Sciences Zoologiques* 106:1-39, plates I-V.

Verdcourt, B. 1974. A new species of *Gulella* Pfeiffer from the Usambara Mountains, Tanzania. *Archiv für Molluskenkunde* 104:57-58.

Verdcourt, B. 1980. Report on the Mollusca collected by Hugh Scott in the Gughé Highlands (Ethiopia), with the description of two new species of *Gulella* (Pulmonata: Streptaxidae). *Journal of Conchology (London)* 30:247-251.

Verdcourt, B. 1990. Two Ethiopian streptaxids (Gastropoda: Pulmonata: Streptaxidae). *Journal of Conchology (London)* 33:345-354.

Verdcourt, B. 1993. A new species of *Gulella* Pfeiffer from southern Tanzania (Mollusca: Streptaxidae). *Archiv für Molluskenkunde* 121:87-89.

Winter, A. J. de. 1996. Six new species of Streptaxidae (Gastropoda Pulmonata) from West Africa. *Basteria* 60:139-148.

Zilch, A. 1959-1960. Gastropoda, Teil 2, Euthyneura, Band 6. *In: Handbuch der Paläozoologie*, O. H. Schindewolf, ed. pp. 1-834. Gebrüder Bornträger, Berlin.

Date of manuscript acceptance: 14 May 1998